
JOURNAL OF THE ARNOLD ARBORETUM

VOLUME 70

JANUARY 1989

NUMBER 1

TAXONOMIC STUDIES IN THE PIPERACEAE—I. THE PEDICELLATE PIPERS OF MEXICO AND CENTRAL AMERICA (PIPER SUBG. ARCTOTTONIA)

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The taxon *Arctottonia*, originally proposed by Trelease as a new genus to accommodate the northern element of Neotropical pipers with pedicellate flowers (*Ottonia*), is recognized as a distinct subgenus within the highly heterogeneous *Piper*. The racemose inflorescence upon which *Arctottonia* and *Ottonia* were previously allied is considered to be a homoplasious character (Callejas, 1986) that occurs in three distinct evolutionary lineages. As currently circumscribed, *Piper* subg. *Arctottonia* is distinguished by its pedicellate flowers arranged in a loose raceme, its tendency toward adnation of the stamens to the ovary, its palmate-veined leaves, and its distribution from central Mexico to northern Central America. Fourteen species are recognized, of which five are described as new. A key is given for the subgenus; descriptions, illustrations, and specimen citations are provided for the species; and an argument is presented for recognizing *Arctottonia* and all other segregates from *Piper* sensu lato at the rank of subgenus.

The Piperaceae Agardh are a large pantropic family of well over 3000 described species, with major centers of diversity in northern South America and Central America in the New World, and Malaysia in the Old (Yuncker, 1958).

The family can be easily recognized on a gross morphological basis. The leaves are always simple and, with rare exceptions, entire; they are usually alternate, although the arrangement is somewhat variable. The flowers are minute, are perfect or unisexual (the plants then typically dioecious), and lack a perianth. The inflorescence (or infructescence) is a compact (or sometimes loose) spike or rarely a raceme. Each flower is subtended by a small, variable bract, and the ovary is unilocular with a single basal ovule. The fruit is a small drupe.

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Despite a considerable amount of attention during the past century and a half, the Piperaceae continue to be taxonomically difficult and enigmatic. The present chaotic taxonomic state of the family is largely a result of its unfortunate past treatment. Nowhere is this more true than for *Piper* L. sensu lato, which is perhaps the largest genus of flowering plants devoid of a natural classification.

The primary reason for this situation is the large number of described species, conservatively estimated at over 1500 for *Piper* alone. Many of these species, especially those established since the turn of the century, have been described without any reference to their putative position within the genus. Several factors have contributed to this artificially inflated species number. First, the flowers are small and the vegetative and floral morphology is uniform throughout the genus (Burger, 1972). Second, species descriptions have often been based on insignificant characters of little taxonomic value, or on fragmentary material often lacking flowers or fruits essential for identification. Third, new species are established based on their occurrence in a distinct political distributional unit, despite their similarity with previously described species. Both C. de Candolle and Trelease (two individuals who had a significant impact on the taxonomy of the family) were especially guilty in this respect, a situation that Standley and Steyermark (1952, p. 229) discussed as follows:

In later years, however, [C. de Candolle], with more abundant material for study, became too enthusiastic in proposing new continental species, and named a very large number without apparent reference to West Indian species, presumably assuming that they must be new because of their remote occurrence. Trelease believed that the species of Piperaceae were extremely local, as many of them are. However, he went still further, and assumed that those of one country were distinct from all those (except a very few widespread and more or less "weedy" species) of the adjoining countries. Such narrow limits of distribution are not found in any other group of Central American plants, nor, in the opinion of the writers, does it exist in the Piperaceae. In his recognition of limiting geographic units, Trelease was scarcely consistent. He treated the whole of Mexico as one Piperaceous unit, and each of the Central American countries as a unit of equal standing. Now each of these Central American countries is about equal in area to one of the states of Mexico, obviously making such an alignment improbable.

Within the last 25 years there have been significant advances toward combating the nomenclatural problems created by this overabundance of names. Much of this progress has been achieved through floristic treatments of specific geographic and/or political units (e.g., in the Neotropics, Burger, 1971; Yunker, 1972, 1973, 1974; Howard, 1973; Steyermark, 1984). Less frequent have been revisions of small segregates from *Piper* sensu lato (Steyermark, 1971; Smith, 1975). While the former method is perhaps more significant from a nomenclatural standpoint in that it tends to include far more taxa (and therefore more names), the latter can accomplish similar nomenclatural results while also addressing questions concerning evolutionary relationships within *Piper*. This paper, which treats the pedicellate pipers of Mexico and Central America, uses the latter approach. The goal is to provide a much-needed update of the taxonomy of this natural group of closely related species, with the ultimate intention of making progress toward a phylogenetic classification of *Piper* sensu lato.

TAXONOMIC HISTORY

Trelease (1921) considered the pedicellate pipers of Mexico and Central America as the North American counterpart to a group of primarily South American species known as *Ottonia* Sprengel or *Piper* subg. *Ottonia* (Sprengel) C. DC. In 1930 he segregated these same northern constituents as the new genus *Arctottonia* on the bases of their distinctive palmate leaf venation, their tendency toward adnation of the stamens to the ovary, and their disjunct distribution.

The first arctottonioid piper was described by Opiz (1828) as *Piper stipulaceum*. Kunth (1839), segregating genera from *Piper* sensu lato, transferred this species to his new genus *Enckea*, even though he characterized *Enckea*, in part, by sessile flowers and fruits.

Miquel (1843–1844), in his monographic treatment of the Piperaceae, shared Kunth's opinion that *Piper* should be divided into several small genera and consequently maintained the placement of *Enckea stipulacea* (Opiz) Kunth. Either Kunth and Miquel did not believe Opiz's original description to be correct with respect to the pedicellate fruits, or they simply chose to ignore this fact. The only other significant nomenclatural change before C. de Candolle assumed the mantle of authoritative monographer of the Piperaceae was Presl's (1851) first combination of an arctottonioid piper in the genus *Ottonia*, creating *Ottonia stipulacea* (Opiz) Presl.

In his monograph for the *Prodromus* (1869), De Candolle relegated all of Kunth's and Miquel's segregate genera to sectional status and/or submerged them in synonymy. His sect. *Enckea*, for example, comprised Kunth's genus *Enckea* and Miquel's genus *Callianira*. His circumscriptions allowed for the inclusion of both pedicellate- and sessile-flowered species in the same section, because he placed more emphasis on the number of stamens and the position of the inflorescence (axillary vs. terminal and leaf opposed). This resulted in the assignment of newly described arctottonioid pipers to his sects. *Enckea* (Kunth) C. DC. (*Piper muelleri* C. DC.) and *Steffensia* (Kunth) C. DC. (*P. neesianum* C. DC.). He also (p. 367) placed *P. stipulaceum* in his category of "species non satis notae, amenta oppositifolia, flores hermaphroditi, americanae," even though Presl's 1851 description of *Ottonia stipulacea* is rather extensive.

For the next 50 years little change in the taxonomy of *Piper* occurred with respect to taxon *Arctottonia*. During this period only one arctottonioid piper was described; *P. yucatanense* was established by De Candolle and assigned to his sect. *Enckea*. Indeed, since the taxonomy of *Piper* remained largely in the hands of De Candolle, his conservative viewpoint prevailed. Even in his later years, De Candolle's static views changed significantly only to the extent that he recognized *Ottonia* as a distinct section that combined the pedicellate members of his sects. *Enckea* and *Steffensia*.

With the influx of material collected in Mexico and Central America during the beginning of the twentieth century, new arctottonioid species were discovered. De Candolle described four such Mexican species, all of which were placed in section *Ottonia*, in 1920 (published posthumously). In his final treatise (De

Candolle, 1923), the key to all known piperaceous taxa, eight species referable to *Arctotonia* were included in *Ottonia*, which he now treated at the level of subgenus.

Trelease (1934, 1935), subsequent to his creation of *Arctotonia*, described three additional species of the genus, all supposedly new to science. Aside from *A. stipulacea* (Opiz) Trel., no other valid combinations have ever been published in *Arctotonia*. In fact, Lundell (1937) soon transferred two of the "new" species to *Piper* because he did not consider the characters used to distinguish *Arctotonia* significant enough to warrant its continuation as a distinct genus.

This sentiment regarding the status of *Arctotonia* has since prevailed. Yuncker (1950) eventually submerged *Arctotonia* under *Ottonia*, stating (p. 71) "it is not believed that the differences upon which Trelease based the genus *Arctotonia* are of generic status." Trelease and Standley (*in* Standley & Steyermark, 1952) did describe another arctotonioid piper as *Piper guazacapanense* but indicated in the key that it belonged, along with two other taxa, to subg. *Arctotonia*.

CLASSIFICATION OF PIPER SENSU LATO

A recent cladistic analysis of the tribe Pipereae (Callejas, 1986 and pers. comm.) confirmed the notions of Kunth and Miquel, among others, that *Piper* sensu lato is a highly heterogeneous assemblage from which segregate taxa should be recognized. One such group is the arctotonioid pipers of Mexico and Central America. Although they share a relatively unusual feature (pedicellate flowers) with *Ottonia*, which undoubtedly led De Candolle, Yuncker, and others to consider them as representatives of the same taxonomic unit, it is now apparent that the arctotonioid pipers are more closely related to another group of Neotropical pipers (i.e., sect. *Enckea*), with which they share the campylodromous or acrodromous leaf venation and a tendency toward adnation of the stamens to the ovary. The racemose inflorescence that had so influenced the thinking of previous monographers is apparently a parallel development that has arisen in three different lineages within *Piper* sensu lato (*Arctotonia*, *Ottonia*, and *Zippelia* Blume, a monotypic Old World taxon).

From the brief history presented in the previous section, it should be apparent that the hierarchical status of segregates from *Piper* sensu lato remains unresolved. The following comments constitute an argument for recognizing these groups at the level of subgenus.

On the one hand, all currently accepted segregates (i.e., *Lepianthes* Raf. (= *Pothomorphe* Miq.), *Macropiper* Miq., *Sarcorrhachis* Trel., and *Trianaepiper* Trel.; excluding, for the moment, *Ottonia*, which has recently been revised by Callejas (1986)) have been recognized at the generic level. This has served to emphasize the distinctiveness of their axillary (or seemingly axillary) inflorescences in contrast to the terminal, leaf-opposed inflorescences for the remaining taxa within *Piper*. However, if the development of axillary inflorescences is such an important evolutionary step, then one would expect these four taxa to be fairly closely related to one another, perhaps defining a distinct lineage within *Piper* sensu lato. To the contrary, current evidence (see Callejas, 1986) indicates that these groups are quite distantly related and that the de-

velopment of an axillary inflorescence is another example of evolutionary parallelism, similar to the situation for pedicellate flowers. Therefore, if one recognizes these four groups as genera, then all other segregates from *Piper* sensu lato must be similarly treated. This, of course, is a valid option, but one that carries with it enormous nomenclatural consequences (hundreds of new combinations would be required) in a family already burdened by such problems.

A more practical option is to consider all segregates as subgenera within *Piper*. This system will not only be the most convenient but will also reflect the evolutionary relationships within *Piper* sensu lato as accurately as a classification at the generic level. The level of recognition here is not nearly as important as recognition itself. As long as the classification system is a relatively stable one with inherent meaning, the hierarchy within that system becomes merely a matter of choice. Therefore, I have chosen to recognize the pedicellate pipers of Mexico and Central America as *Piper* subg. *Arctotonia*, which agrees with the choice of Callejas (1986 and pers. comm.) for the ottonioid pipers (*Piper* subg. *Ottonia*) and thereby initiates what we hope will be the beginning of a more stable and meaningful infrageneric classification for the genus *Piper*.²

HABITAT AND GEOGRAPHIC DISTRIBUTION

Members of the genus *Piper* are common understory shrubs or small trees of various habitats but are best represented in lowland tropical rainforests. As such, most species prefer moist forest formations below 1000 m alt. Nevertheless, a considerable number of them, including the majority of species in *Piper* subg. *Arctotonia*, can tolerate the seasonally dry subdeciduous to deciduous tropical forests.

With a few notable exceptions the species in subg. *Arctotonia* occupy relatively open, often disturbed sites at the edge of primary forests, being frequent inhabitants of steep banks and stream sides. Because they are able to withstand these disturbed conditions, and with the increased destruction of the tropical forests by man, many of these species are able colonists of what would be considered second-growth forests.

The arctotonioid pipers can be subdivided geographically into two major groups. The vast majority of species occur in a zone between the coast and the foothills of the western Sierra Madre, from Sinaloa in the north to Chiapas and Guatemala in the south. The remaining three species occupy the eastern portions of Mexico, within or east of the Sierra Madre Oriental from central Veracruz to the Yucatán Peninsula, continuing into neighboring Honduras, with isolated collections from the lowlands of southeastern Nicaragua and central Panama. This geographic distinction is highly correlated with leaf shape: broadly ovate to suborbiculate and commonly cordate at the base in species from the "western assemblage," and narrowly ovate-lanceolate or narrowly elliptic with a long-acuminate apex in those of the "eastern assemblage" (see FIGURE 1).

²For the four generic segregates mentioned, most of the ca. 40 species within these groups have been treated at one time or another as members of the genus *Piper*. Therefore, relatively few new combinations would be required to treat these groups appropriately at the rank of subgenus.

At low elevations near the coast in Nueva Galicia (see Rzedowski & McVaugh, 1966, for a definition of this area), several members of the "western assemblage" (*Piper brachypus* Trel., *P. brevipedicellatum* Bornstein, *P. rosei* C. DC., and *P. stipulaceum*) are common inhabitants of the palm forests dominated by *Orbignya cohune* (C. Martius) Dahlgren ex Standley. At slightly higher elevations and often farther inland, these same species are joined or replaced by other pedicellate pipers (*P. abalienatum* Trel. and *P. novogalicianum* Bornstein) and occupy sites in the disturbed semideciduous forests dominated by *Brosimum alicastrum* Sw., *Hura polyandra* Baillon, and species of *Ficus* L. and *Bursera* Jacq. ex L. Still other species in this group, including *P. colotlipanense* Bornstein from the state of Guerrero and *P. guazacapanense* from Chiapas and neighboring Guatemala, occur in seemingly stable and mesic environments in more remote localities.

Within the "eastern assemblage," the dominant and widely distributed *Piper neesianum* C. DC. and *P. yucatanense* are native to the "ramonales" forests of the Yucatán Peninsula, upland, climax, subdeciduous forests developing on calcareous soils and dominated by the breadnut tree, *Brosimum alicastrum*. However, the influence of man in these once relatively unoccupied regions has all but destroyed these primary forests, at least in Mexico. Fortunately, these two species (especially *P. neesianum*) have adapted as able colonizers of disturbed sites to remain fairly conspicuous elements of the second-growth forests that now dominate this area.

HABIT

With the single known exception of *Piper guazacapanense*, all members of *Piper* subg. *Arctotonia* are erect plants. They are 0.5–6.5(–9) m tall and 0.5–7.5 cm in diameter at the plant base; the most common forms are shrubs and slender treelike specimens. All of the species are woody with conspicuously nodose stems (a common feature for the genus), although the amount of wood developed in some species, especially the prostrate *P. guazacapanense*, is minimal. Since the inflorescences in subg. *Arctotonia* are terminal and leaf opposed, continued apical growth is assumed by the apical bud, resulting in a sympodial growth pattern.

MEASUREMENTS AND TERMINOLOGY

Information provided in the key and descriptions was obtained from the study of herbarium specimens, fluid-preserved materials (especially flowers and fruits), and notes made in the field. Voucher specimens of my own collections have been deposited at MICH, with complete or partial sets distributed to the following herbaria (cited according to Holmgren *et al.*, 1981, and in order of distribution): MEXU, CHAP, INIF, GH, NY, CAS, DUKE, F, and MO.

The terminology used to describe the various plant features generally follows that of Radford *et al.* (1974). With the exception of a few pickled fruits, all measurements have been taken directly from herbarium specimens. In some

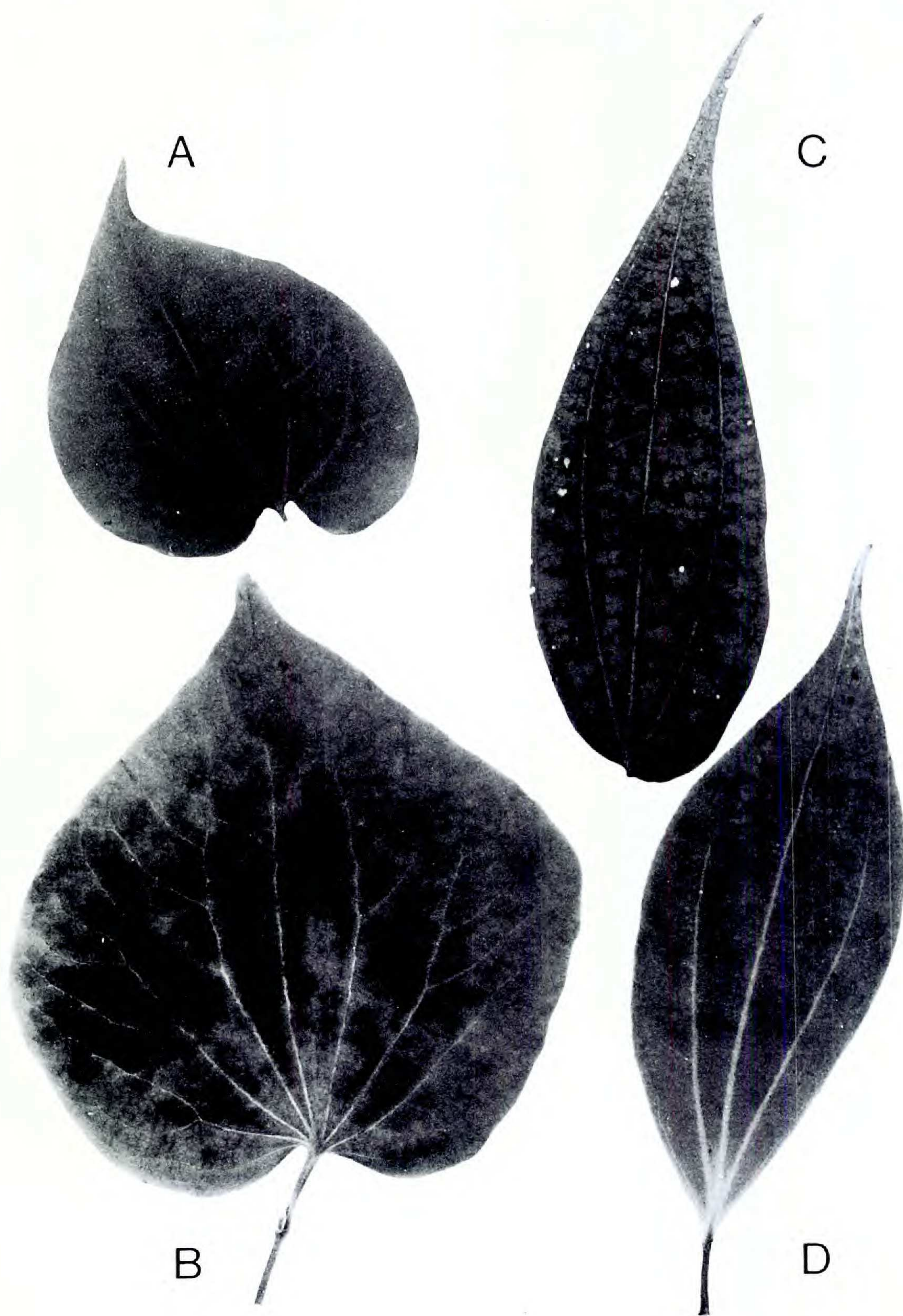


FIGURE 1. Major leaf shapes in *Piper* subg. *Arctottonia*. A, B, broadly ovate to sub-orbicular, commonly cordate at base: A, *P. guazacapanense*; B, *P. abalienatum*. C, D, narrowly ovate-lanceolate or narrowly elliptic with long-acuminate apex: C, *P. yucatanense*; D, *P. neesianum*.

instances flowers were placed in a weak detergent mixture to soften them in order to count the number of stamens and stigma lobes more accurately.

Whenever possible, ten measurements were made from each collection number in an attempt to obtain a reasonable sample size and to document any variation that may exist within a single collection. Obviously immature or incomplete structures were avoided. Measurements of inflorescence length include the peduncle, since it was not always possible to separate the peduncle from the flowering rachis accurately.

A scanning electron microscope was used to observe details of the leaf surface (e.g., hair type) and various floral characteristics. This was facilitated by critical-point-drying the materials pickled in the field in order to retain their shape during the drying process.

Certain terms referring to the hairs and their overall appearance are used here in a relative manner:

puberulent—having very short (generally less than 0.1 mm), glandular or eglandular hairs barely visible at 10× magnification.

pubescent—similar to puberulent, but with the eglandular hairs noticeably longer (ca. 0.1–0.3 mm long) and generally visible to the unaided eye.

long-pubescent—similar to pubescent, but with the hairs 0.3–0.5 mm long.

densely pubescent—similar to pubescent, but with the hairs more numerous and therefore easily visible to the unaided eye. (This is obviously a subjective distinction. Quite often, densely pubescent and long-pubescent are correlated features.)

MORPHOLOGY

LEAVES

The leaves of *Piper* subg. *Arctottonia*, like those of the vast majority of pipers, are alternate, simple, and entire margined. As briefly discussed above, two distinct groups occur with respect to shape: those with leaves conspicuously longer than broad and lance-elliptic to elliptic-ovate, and those with leaves more nearly equal in length and width and broadly to very broadly ovate or suborbiculate (see FIGURE 1). The apex is predominantly acuminate, either long or short, while the base varies from cuneate to rounded or cordate. In some specimens of *P. yucatanense* and *P. neesianum*, the base is slightly oblique. Leaves are membranous in all species of subg. *Arctottonia* except *P. neesianum*, in which they are coriaceous, especially upon drying.

According to the terminology associated with Hickey's (1979) classification of the architecture of dicotyledonous leaves, the most prevalent venation pattern in subg. *Arctottonia* is acrodromous, with basal position and perfect development. In some species with cordate leaf bases, especially *Piper guazacapanense*, campylodromous venation is commonly found. The number of major veins varies from 3 to 9 (to 11), depending to a large degree on the width of the leaves, but only the three most central ones project into the acumen. The secondary veins are irregularly spaced, although in some species they form a series of interconnecting arches near the margin. Tertiary and higher-order veins form a random reticulation.

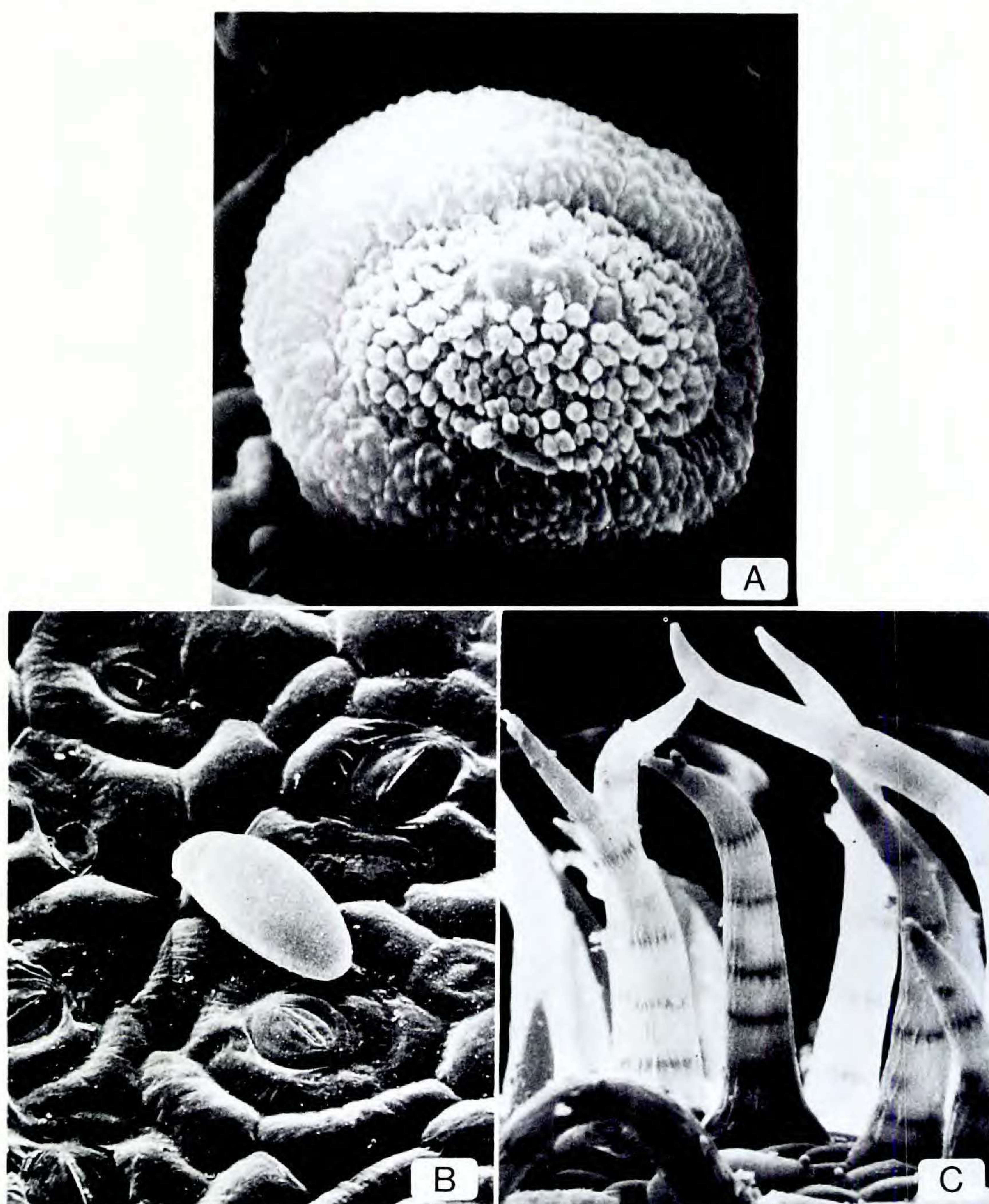


FIGURE 2. A, pollen grain of *Piper abalienatum*, representative of subg. *Arctottonia*, $\times 3850$. B, C, hair types in *Piper* subg. *Arctottonia*: B, bicellular, glandular hair with short stalk cell and ellipsoid gland cell (*P. novogalicianum*), $\times 550$; C, multicellular, uniseriate, eglandular hair (*P. stipulaceum*), $\times 275$.

INDUMENTUM

Two hair types occur in subg. *Arctottonia* that I term glandular and eglandular. The glandular hairs are bicellular, with a small stalk cell subtending a larger, ellipsoid gland cell (see FIGURE 2B). These hairs are quite small (up to $35\ \mu\text{m}$) and are therefore easily overlooked. On mature leaves they are often absent or very sparse. They usually occur on both surfaces of the leaves, and

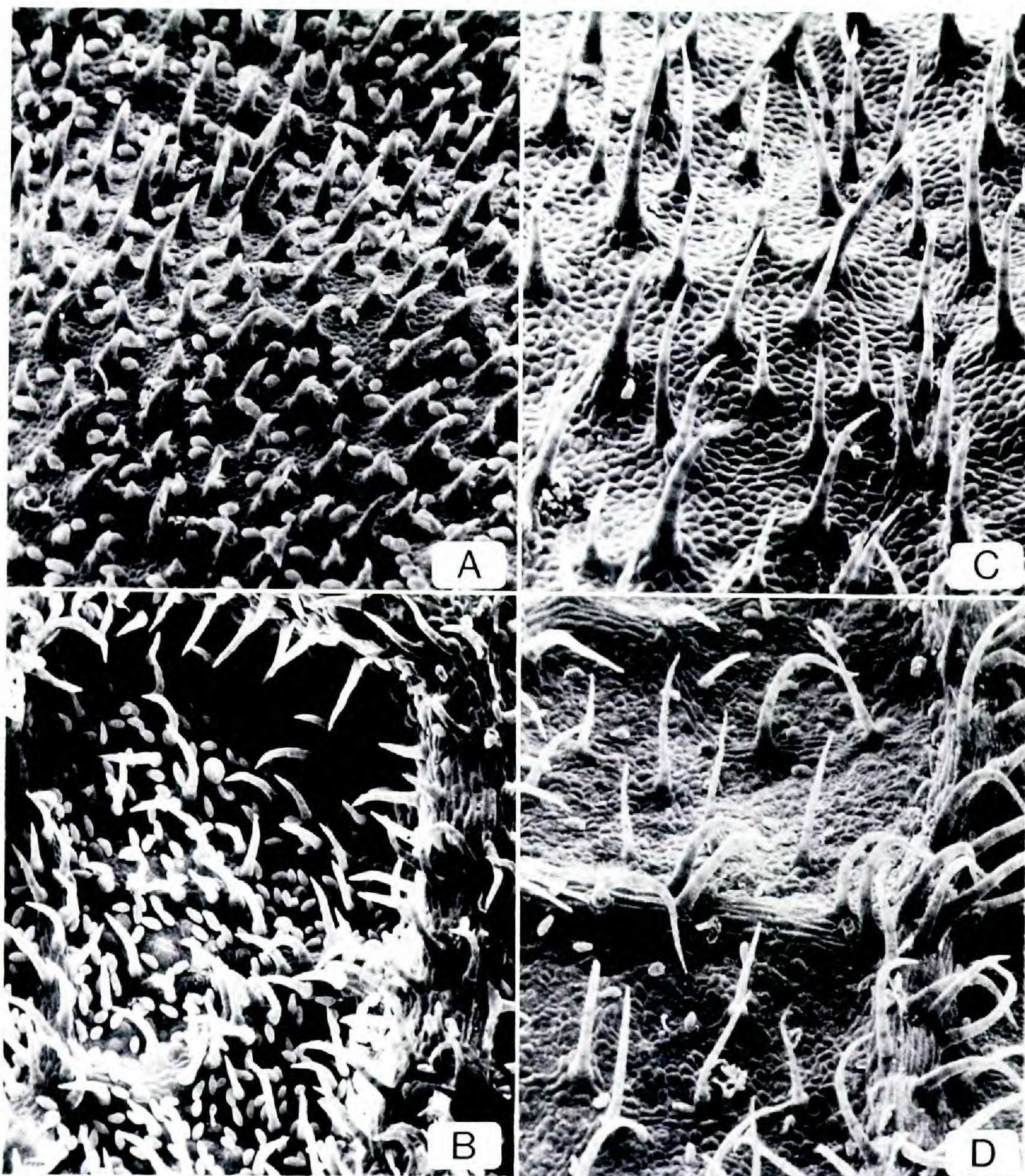


FIGURE 3. Distribution of hair types in *Piper* subg. *Arctottonia*, as seen on leaves of *P. stipulaceum*: A, upper surface, immature specimen, $\times 60$; B, lower surface, immature specimen, $\times 60$; C, upper surface, mature specimen, numerous eglandular hairs and sparse glandular ones (compare with A), $\times 55$; D, lower surface, mature specimen, eglandular hairs mainly on veins, $\times 60$.

they are quite commonly more numerous beneath, being especially concentrated in the regions between veins (see FIGURE 3).

The eglandular hairs are simple, unbranched structures. They are always multicellular, uniseriate, broadened at the base, and gradually tapered to an acute apex (see FIGURE 2C). The number of cells differs with hair length, which in turn is quite variable within a specimen. Hairs as long as 0.5 mm have been recorded in *Piper colotlipanense* and *P. abalienatum*, but approximately 0.1–0.3 mm is more normal. Like glandular hairs, eglandular ones are usually more

abundant on the lower leaf surface; in contrast, however, they are more frequent on—and at times restricted to—the veins (see FIGURE 3).

On a gross level these hairs, especially the more conspicuous eglandular ones, produce surfaces ranging from sparsely puberulent to tomentose. The degree of pubescence and the distribution of hairs, in correlation with floral features, are quite useful in delimiting species (but see comments in the introduction to the taxonomic treatment).

PROPHYLLS

An interesting vegetative structure associated with the newly developing leaf and inflorescence is the prophyll. Technically, a prophyll is the “first leaf or one of two first leaves” of an axillary shoot (Esau, 1977, p. 522). In essence, prophylls are reduced leaves that subtend lateral branches, often occurring in odd positions and thus not conforming to the normal phyllotaxy of the shoot. In dicots there are usually two prophylls, whereas in monocots there is only one (Eames, 1961).

In *Piper* only one prophyll occurs, and according to Burger (1972), who has surveyed this character in several Costa Rican species, its development relative to the leaf base and axillary shoot is variable. On the basis of his study, he tentatively concluded that developmental differences, together with prophyll morphology and floral features, may suggest natural groupings in *Piper*.

In subg. *Arctottonia* the prophyll always functions to protect the developing axillary shoot by surrounding the new leaf (and inflorescence, if present) in a manner similar to the stipule in *Ficus* or the bud scale in *Magnolia* L. It is always apically acute and basally truncate, appearing triangular to widely deltate when laid flat. It may be glabrous (or appear so to the naked eye) but more often is abaxially pubescent.

Although this general characterization of the prophyll in subg. *Arctottonia* is consistent from one taxon to another, its similar occurrence in other taxa with different floral morphologies suggests, as Burger pointed out, that the apically acute prophyll has probably evolved independently along several distinct evolutionary lines. Nevertheless, it does help to define subg. *Arctottonia* since it correlates with other features such as racemose inflorescences and palmate leaf venation.

INFLORESCENCES

The inflorescence in subg. *Arctottonia* is unusual in that the flowers are borne on short pedicels. Therefore, the inflorescence is technically a raceme rather than a spike, as in the majority of pipers. As mentioned previously, this inflorescence type is shared with the South American–West Indian *Piper* subg. *Ottonia* and a single Old World species, *P. begoniaefolium* (Blume) Quis.

The length of the pedicel varies from commonly less than 0.5 mm in *Piper brachypus*, *P. brevipedicellatum*, and *P. mcvaughii* Bornstein to usually 1–3 mm in the remaining taxa. Within a specimen variation can be quite noticeable, especially when one compares flowering and fruiting pedicels. Apparently, in many cases, the pedicel continues to elongate as the flower matures. At the

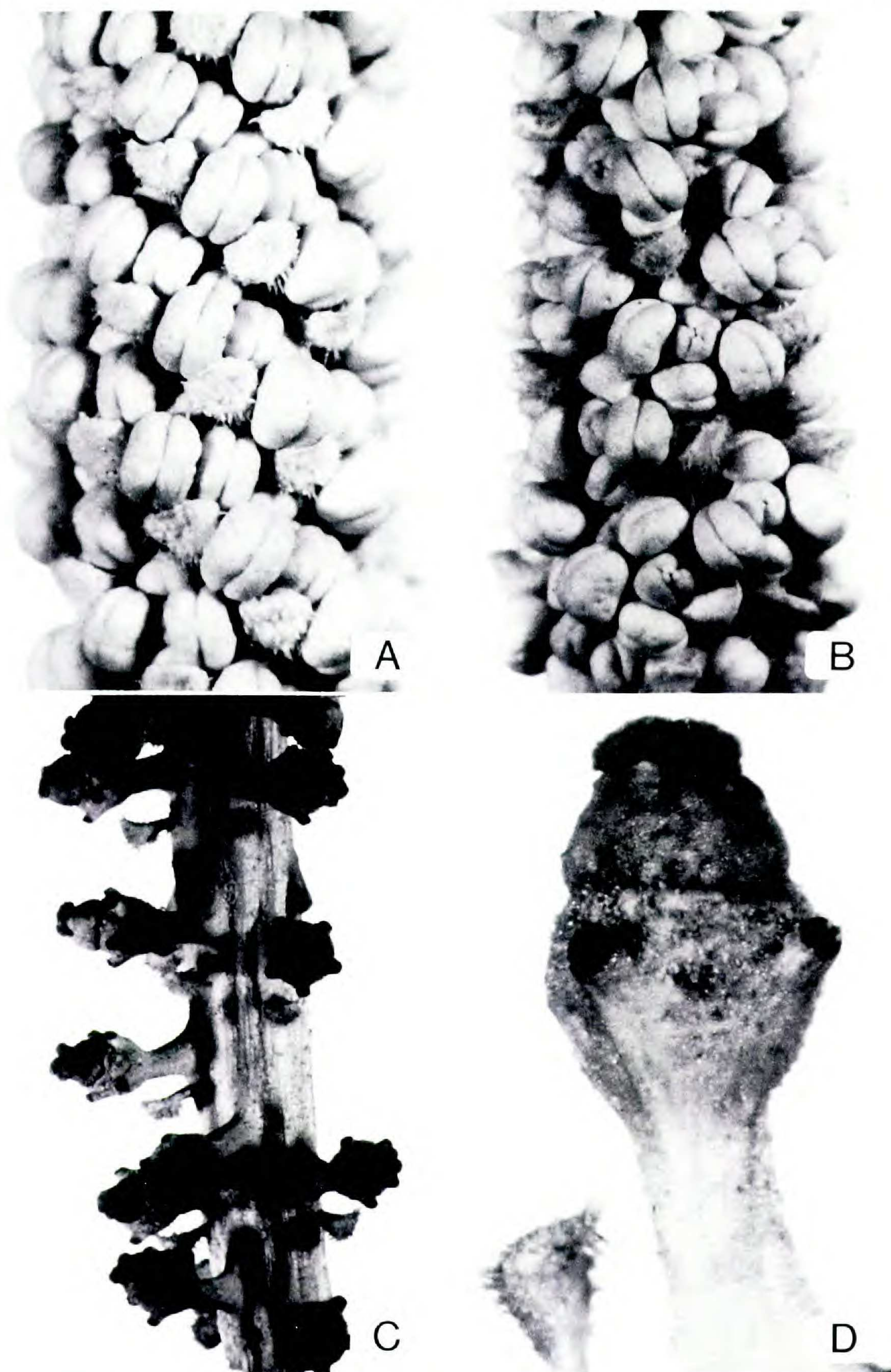


FIGURE 4. Basic floral features in *Piper* subg. *Arctottonia* and morphological changes occurring during development, as seen in *P. stipulaceum*: A, immature inflorescence,

same time, the maturing fruit expands and the receptacular portion of the pedicel swells, making it very difficult to determine the exact position of the pedicel-fruit junction. These developmental changes can create significant problems in identification, especially for material in early flower, since the pedicels are immature (see the developmental series in FIGURE 4). It is therefore more reliable, in my opinion, to examine young fruiting specimens for positive identification.

The inflorescence axis is rather narrow (rarely more than 2 mm) in all species. The peduncle is often slightly broader than the remaining rachis, but it is a gradual change of no apparent significance. The rachis is glabrous or, more commonly, puberulent to pubescent with eglandular and/or glandular hairs. This feature is useful in helping to delimit species.

FLORAL BRACTS

This character was an integral feature in Miquel's subdivision of *Piper* sensu lato into segregate genera. According to Callejas (1986), variation in bract shape is useful in helping to delimit taxonomic groups within *Piper*.

In subg. *Arctotonia* the floral bracts do not form a banded pattern. They are generally spatulate to spatulate-cupulate (otherwise described as conchaeform, shell-like, or conical at the expanded apical region). In some species the broadened apex narrows at the base to form a distinct petiole, whereas in others the bract is essentially sessile on the inflorescence rachis. The bracts may be completely glabrous (*Piper neesianum*), to sparsely puberulent (*P. mcvaughii*), to densely pubescent (*P. brachypus*, *P. colotlipanense*, and *P. brevipedicellatum*). Usually the hairs are present only on the abaxial surface or at the bract margin, and they may be eglandular (most common) and/or glandular. These variations prove useful at the species level.

FLOWERS

The flowers are very simple structures consisting only of the male and female reproductive parts (see FIGURE 4). A perianth is completely lacking. The androecium consists of (3 or) 4 to 6 (or 7 to 9) stamens, which may be attached immediately beneath the single ovary (hypogynous) or may, in a very few species (*Piper abalienatum*, *P. stipulaceum*, and *P. mcvaughii*), be adnate to it. In several taxa there appears to be a tendency toward adnation of the stamens to the lower portion of the ovary. This may simply be a developmental anomaly associated with fruit ripening and expansion, which involves the upper (receptacular) portion of the pedicel. In other cases the lower portion of the filaments appears to be fused to the ovary wall, with the free section therefore arising a

bracts readily visible (note protandrous development of flowers), $\times 18$; B, slightly more mature inflorescence, floral bracts becoming obscured by expanding flowers, gynoeceum now evident, $\times 15$; C, young infructescence, pedicels now conspicuous, bract shape more apparent, stamen position and number more readily determined, $\times 7$; D, single young fruit and associated bract, adnation of stamens to ovary evident, $\times 21$.

short distance from the apparent ovary base. For convenience I have chosen to refer to these stamens as hypogynous. When this tendency is especially strong, I have mentioned it in the species description or in the accompanying discussion.

The filaments vary but in most cases are less than 0.5 mm long. In *Piper abalienatum*, *P. colotlipanense*, and *P. muelleri* C. DC., the filaments are particularly long, often exceeding 1 mm. In all taxa the anthers dehisce by longitudinal slits. These are usually oriented laterally, a condition considered primitive by Burger (1972), although in several species there is often a slight change toward upward dehiscence. This is accomplished by an expansion of the connective at the base of the sporangial pairs, the anthers being tetrasporangiate. Burger (p. 360) has postulated that this change in anther orientation, in association with the congestion of the flowers and the compaction of the floral parts, is a response to "the activity of small pollen-collecting bees" (but see also comments by Callejas (1986) regarding floral ontogeny).

The pollen in subg. *Arctottonia* is constant within and between species. The following description employs Walker and Doyle's (1975) terminology. Scanning electron micrographs (FIGURE 2A) clearly indicate that the pollen grains are monosulcate. If the prevailing assumption is made, as Walker and Doyle (1975) suggested, that the aperture is distal-polar, then the grains would be more precisely classified as anasulcate. The exine sculpturing is verrucate, with the sulcus membrane appearing gemmate (described by Erdtman (1966) as granular). The pollen grains are minute to small (ca. $12.75 \times 11.75 \mu\text{m}$) and globose-subspheroidal. This description is in general agreement with that of Walker (1976) for the Piperaceae, providing further evidence that pollen morphology in the family is a relatively invariable feature and therefore of little or no taxonomic value at the level of species.

The gynoecium in all pipers is a single pistil with one locule and one basal orthotropous ovule. The number of carpels that form the gynoecium has long been a source of disagreement. Baillon (1872) interpreted the ovary as unicarpellate. Primarily on the basis of the number of stigmatic lobes, Rendle (1925), Lawrence (1951), and others have suggested that it is 2- to 5-carpellate. Evidence from carpellary vascular bundles indicates a tricarpetate derivation (Johnson, 1902; Murty, 1959). More recent developmental studies (Tucker, 1982) further substantiate the tricarpetate theory but do not eliminate the possibility of four carpels developing (e.g., *Piper amalago* L., a taxon within subg. *Enckea*, the sister group to subg. *Arctottonia*). Callejas (1986) has also shown that in *Piper* subg. *Ottonia*, four carpels per flower is the rule. Unfortunately, this feature was not critically examined in my study. Stigma branches—a fairly reliable criterion in *Piper* for judging the number of carpels—were counted, with values ranging from 3 to 5 (3 and 4 predominating). However, the number of stigmatic lobes varies within a single inflorescence, which strongly suggests that this feature is of little value in delimiting species. Its usefulness at higher taxonomic levels is still in question.

In the majority of *Arctottonia* species, the ovary is ovoid-ellipsoid, with prevailing tendencies toward globose. The most notable exception occurs in *Piper muelleri*, where the ovary is conspicuously depressed-ovoid, accentuated

by the long staminal filaments and the elongate style. The style is a variable feature important in some cases in helping to distinguish between species. It is often depressed-ovoid but varies continuously to conical (*P. stipulaceum*, *P. colotlipanense*, *P. neesianum*) or columnar (*P. abalienatum*, *P. mcvaughii*). Associated with this change is an increase in the length ratio of style to ovary in the flowering condition from approximately 1:3 to 3:2. At maturity the stigma lobes are papillose, with numerous clavate or columnar hairs. With the exception of *P. muelleri* and the occasional specimen of *P. abalienatum*, where they are recurved, the stigma branches are short and flattened on the style.

FRUITS

The fruit in *Piper* is a small drupe with scant endosperm and abundant perisperm. It is most often globose, varying to ellipsoid (*P. yucatanense*), ovoid-ellipsoid (*P. neesianum*), and obloid (*P. stipulaceum*), and is small ($2-3 \times 1.5-2.5$ mm). In most species the fruit is capped by the persistent style (see FIGURE 4), and glandular hairs are present to some degree. So far as is known, the fruit is opaque, either brown or black, except in *P. guazacapanense*, where it is a translucent pearl-white.

TAXONOMIC TREATMENT

The circumscription of taxa and the identification of specimens in *Piper* subg. *Arctottonia* have been complicated by changes that occur as a result of plant maturation. Vegetatively, this is usually manifested by a change in leaf and hair size, as well as the eventual loss of the hairs (especially the glandular ones) in the most mature specimens (see FIGURE 3). Florally, it involves the length of the inflorescence and the pedicels, the degree of pubescence on the bracts, the size and shape of the ovary, and the expansion of the ovary during fruit formation, which may, in turn, affect the position of the stamens and the appearance of the style (see FIGURE 4).

In the past the phenotypic differences caused by these changes were not linked to developmental phenomena, and some of them led to the misidentification of specimens or were considered significant enough to warrant the establishment of new species. In this study many of these developmentally induced variations have been discovered by collecting materials from the same individual at different stages of maturation. This has allowed me to observe these changes over time and thereby eliminate the confusion that often results when examining collections from different plants. I have thus been able to identify most specimens at a single, specific stage of maturation by comparing their appearance with "known" specimens. Unfortunately, this was not possible for all of the taxa that I have recognized. In these cases I have resorted to the standard practice of equating differences (discontinuities) with distinct species.

Piper subg. **Arctottonia** (Trel.) Standley & Steyerl. Fieldiana, Bot. **24**(3): 275. 1952.

Arctottonia Trel. Proc. Amer. Philos. Soc. **69**: 315. 1930. TYPE: *Piper muelleri* C. DC.

Shrubs or small trees, occasionally scandent or subherbaceous, terrestrial, the stems conspicuously nodose; plants glabrous or variously pubescent, the hairs bi- and/or multicellular, glandular or not. Prophyll single, lateral, triangular, forming cocoonlike structure enclosing and protecting developing shoot apex. Leaves alternate; petiole vaginate at base, without ligulate process; blade simple, entire, palmatinerved, acrodromous or campylodromous. Inflorescences terminal, leaf-opposed, more or less loosely flowered racemes, erect (or rarely pendent?); floral bracts petiolate or sessile, spatulate to strongly spatulate-cupulate, not forming bands at any stage of development. Flowers small, perfect; perianth absent; stamens 4 to 6 (to 9), the filaments to 1 mm long, rarely longer, the anthers ovoid to subglobose, bithecate, tetrasporangiate, dehiscent by longitudinal slits; ovary superior or with stamens variously adnate, unilocular with single, basal, orthotropous, bitegmic ovule, style present or absent, stigma lobes (2 or) 3 or 4 (to 6). Fruit a small drupe, fleshy or dry, ovoid to globose, smooth or distinctly ribbed or angled; seeds with much perisperm and little endosperm.

This subgenus constitutes a natural assemblage of 14 species confined to Mexico and Central America. The primary center of diversity is in west-central Mexico (Nueva Galicia); a second subgroup of three species, two of which are rather widespread, occurs from central Veracruz, Mexico, through the Yucatán Peninsula (Mexico, Guatemala, and Belize) to neighboring Honduras, with isolated plants in Nicaragua and Panama.

KEY TO THE SPECIES OF PIPER SUBG. ARCTOTTONIA³

1. Leaves 1.5–3 times longer than broad, lance-elliptic to narrowly ovate, the base cuneate-attenuate to rounded, very rarely slightly cordate.
 2. Rachis puberulent or densely pubescent with eglandular hairs; floral bracts pubescent to densely pubescent.
 3. Leaves pubescent beneath, especially along major veins; filaments 0.5–1 mm long; rachis puberulent; fruits depressed-ovoid to globose. . . . 9. *P. muelleri*.
 3. Leaves glabrous to sparsely puberulent at petiole-blade junction; filaments < 0.25 mm long; rachis densely pubescent; fruits ellipsoid to obovoid to subglobose. 4. *P. cihuatlanense*.
 2. Rachis and floral bracts glabrous.
 4. Leaves chartaceous to coriaceous, shiny green above, gray-green to silvery beneath, nonrugulose; plant a dense shrub to 6.5 m tall; fruits ribbed; floral bracts < 0.5 mm long. 10. *P. neesianum*.
 4. Leaves membranous, dull green on both surfaces, generally drying rugulose; plant a loosely branched shrub to 3 m tall; fruits smooth; floral bracts 0.25–1.5 mm long. 14. *P. yucatanense*.
1. Leaves usually 1–1.5 times longer than broad, ovate to broadly ovate to suborbiculate, the base usually distinctly cordate, sometimes truncate to rounded.
 5. Stamens conspicuously adnate to ovary, often near middle.

³Although it is possible to recognize two distinct lineages or subgroups within *Piper* subg. *Arctottonia*, interspecific relationships are more ambiguous since the polarity of certain character states is conjectural at best. For that reason, a formal phylogeny for subg. *Arctottonia* is not presented at this time, and the species in the following taxonomic treatment are arranged alphabetically. Comments concerning putative relationships can be found in the discussions that accompany each description.

6. Pedicels to 0.5 mm long, rarely longer; leaves 5.1–8 × 5.5–7.6 cm, sparsely puberulent beneath with short eglandular hairs. 7. *P. mcvaughii*.
6. Pedicels (0.5–)1–2(–3) mm long; leaves (4.5–)6.3–20.4 × (4.8–)6.5–19.8(–21) cm, puberulent to tomentose beneath.
 7. Style columnar to very long-conical, 0.5–2 mm long, as long as ovary in flower, $\frac{1}{3}$ – $\frac{1}{2}$ as long in fruit; filaments 0.5–1 mm long; ovary ovoid-ellipsoid; stamens occasionally in 2 whorls. 1. *P. abalienatum*.
 7. Style depressed-ovoid to short-conical, to 0.5 mm long, from $\frac{1}{3}$ to equal ovary length in flower, $\frac{1}{5}$ – $\frac{1}{3}$ as long in fruit; filaments to 0.5 mm long; ovary ovoid to globose; stamens in single whorl. 13. *P. stipulaceum*.
5. Stamens hypogynous or sometimes appearing adnate to base of ovary due to its expansion in fruit.
 8. Plant a prostrate, creeping subshrub, periodically rooting at nodes; fruits pearl white, translucent; inflorescences < 4.5 cm long, few-flowered. 6. *P. guazacapanense*.
 8. Plant an erect shrub, never rooting at nodes; fruits green to black, opaque; inflorescences > 5 cm long, many-flowered.
 9. Prophylls, petioles, and leaf blades glabrous (to puberulent or very rarely sparsely pubescent).
 10. Rachis and floral bracts glabrous to sparsely puberulent, rarely with few scattered eglandular hairs; pedicels usually 1.5–2.5 mm long. 8. *P. michelianum*.
 10. Rachis and floral bracts puberulent to more commonly pubescent or densely pubescent with eglandular hairs; pedicels 0.5–1.5 mm long, rarely longer, or flowers subsessile.
 11. Flowers subsessile, the pedicels to 0.5 mm long, rarely longer. 2. *P. brachypus*.
 11. Flowers with pedicels 0.5–1.5 mm long. 12. *P. rosei*.
 9. Prophylls, petioles, and leaf blades pubescent to densely pubescent or tomentose (rarely only puberulent).
 12. Pedicels generally < 0.5 mm long, stout, about as long as broad. 3. *P. brevipedicellatum*.
 12. Pedicels generally > 1 mm long, as long as—or, more commonly, distinctly longer than—broad.
 13. Filaments 0.5–1 mm long; young twigs, petioles, leaf blades, and prophyll densely long-pubescent to tomentose. 5. *P. colotlipanense*.
 13. Filaments to 0.5 mm long; young twigs, petioles, leaf blades, and prophylls puberulent to densely pubescent. 11. *P. novogalicianum*.

1. **Piper abalienatum** Trel. Amer. J. Bot. 8: 216. *pl.* 8, *fig.* 1. 1921. TYPE: Mexico, Colima, Colima, July and Aug. 1897, *Palmer 100* (holotype, US!; isotypes, A!, MICH!, UC!). FIGURE 5.

Piper el-muletonum C. DC. Candollea 1: 72, 246. 1923, *nomen nudum*. *Piper el-muletonum* C. DC. ex L. J. Schroeder, Candollea 3: 137. 1926. TYPE: Mexico, Michoacán, El Muleto, 850 m, 30 June 1898, *Langlassé 215bis* (holotype, G!).

Medium-sized shrub, sparsely branched from base, appearing treelike, 1.5–4 m tall; youngest twigs lime green, densely pubescent, becoming glabrous, brown, and eventually light gray with warty lenticels; older stems with conspicuous swollen nodes, maximum diameter to 6 cm. Prophylls to 1.5 cm long

at maturity, base truncate, apex acute, dorsally densely pubescent to tomentose. Leaves with petiole 1–4.5 cm long, stout, densely soft-pubescent with eglandular hairs; blade broadly ovate to orbiculate to occasionally depressed-ovate, 7.1–20.4 × (6.5–)7.6–19.8(–21) cm, rounded to distinctly cordate at base, gradually to abruptly acuminate at apex, (5- to) 7- to 9- (to 11-)nerved, puberulent to pubescent (rarely almost glabrous) above, densely soft-pubescent to tomentose (rarely glabrous to puberulent) beneath with eglandular hairs more prominent on slightly elevated major veins. Inflorescences (4.8–)5.7–15.2 cm long, green when young, turning yellow-white at maturity; peduncle stout, pubescent at base, remaining rachis glabrous or minutely puberulent with glandular hairs; bracts to 1.25 mm long (usually ca. 0.75 mm), narrow petiolate basal portion broadening gradually to abruptly into spatulate to spatulate-cupulate apical region, abaxially sparsely pubescent to pubescent. Flowers with pedicel (0.5–)1–2(–3) mm long, to 1 mm in diameter, glabrous to sparsely puberulent with glandular hairs; stamens (4 or) 5 to 7 (or 8), adnate to near middle of ovary, occasionally appearing as if in 2 alternating whorls, the filaments elongate (to 1 mm), the anthers equal to or slightly shorter than filaments, dehiscing somewhat to conspicuously divergent upward from lateral; ovary ovoid-ellipsoid, 1–2 times as long as style, puberulent with glandular hairs, the style columnar to slightly conical, (0.5–)1–1.5(–2) mm long, persistent in fruit, the stigma 3- to 5-lobed. Fruits globose, to 2 mm in diameter, drying brown to black, with glandular hairs still present.

DISTRIBUTION. Confined to small area in west-central Mexico from southwestern Jalisco, along western side of Sierra Madre, through state of Michoacán (see MAP 1). Although not known from Guerrero, to be expected there, especially at mid-elevations in Sierra Madre del Sur.

HABITAT. Dense shade of mixed deciduous forests, 100–1000 m alt.; often associated with various Leguminosae, Moraceae (especially species of *Brosimum* Sw. and *Ficus*), Euphorbiaceae (*Hura* L.), *Bursera*, and *Malpighia* L. Always grows where water plentiful at some time of year; most abundant at edge of ravines above intermittent mountain streams.

PHENOLOGY. Flowering late May through July, most reliably in June. Young fruits beginning in late June; specimens with mature fruits collected as late as mid-October.

REPRESENTATIVE SPECIMENS.⁴ **Mexico.** JALISCO: 1 km E of El Divisadero (1 km W of Villa Guerrero), 18 km ESE of Tomatlán, *Iltis & Nee 1650* (NY); Estación de Biología de Chamela, *Pérez & Sarukhán 1354* (MEXU, MICH); 15 mi SSE of Autlán on trail between Chante and Manantlán, *Wilbur 2105* (MICH). COLIMA: 2.3 km E on Hwy. 70 toward Ixtlahuacán, *Bornstein 90* (MICH); mountain trail S of Los Tepames, *Bornstein & Hensold 18* (MICH); 5.7 km S of Los Tepames on gravel road to Las Tinajas, *Bornstein & Hensold 21* (MICH); just beyond km 190 and before Río Tuxpan bridge on old Hwy. 110 between Colima and Pihuamo, *Bornstein 91* (MICH); ca. 18 road mi E of Colima, near bridge of Río Tuxpan, km 189, *McVaugh 15498* (MICH); ca. 11 mi SSW of Colima on Manzanillo road, *McVaugh 15564* (MICH); gorge of Río Cihuatlán, near bridge 13 mi N of Santiago, *McVaugh 15809* (MICH). MICHOACÁN: 3.5 mi N of San Juan de Lima on Hwy. 200,

⁴A complete list of collectors for the entire study is given in the appendix.

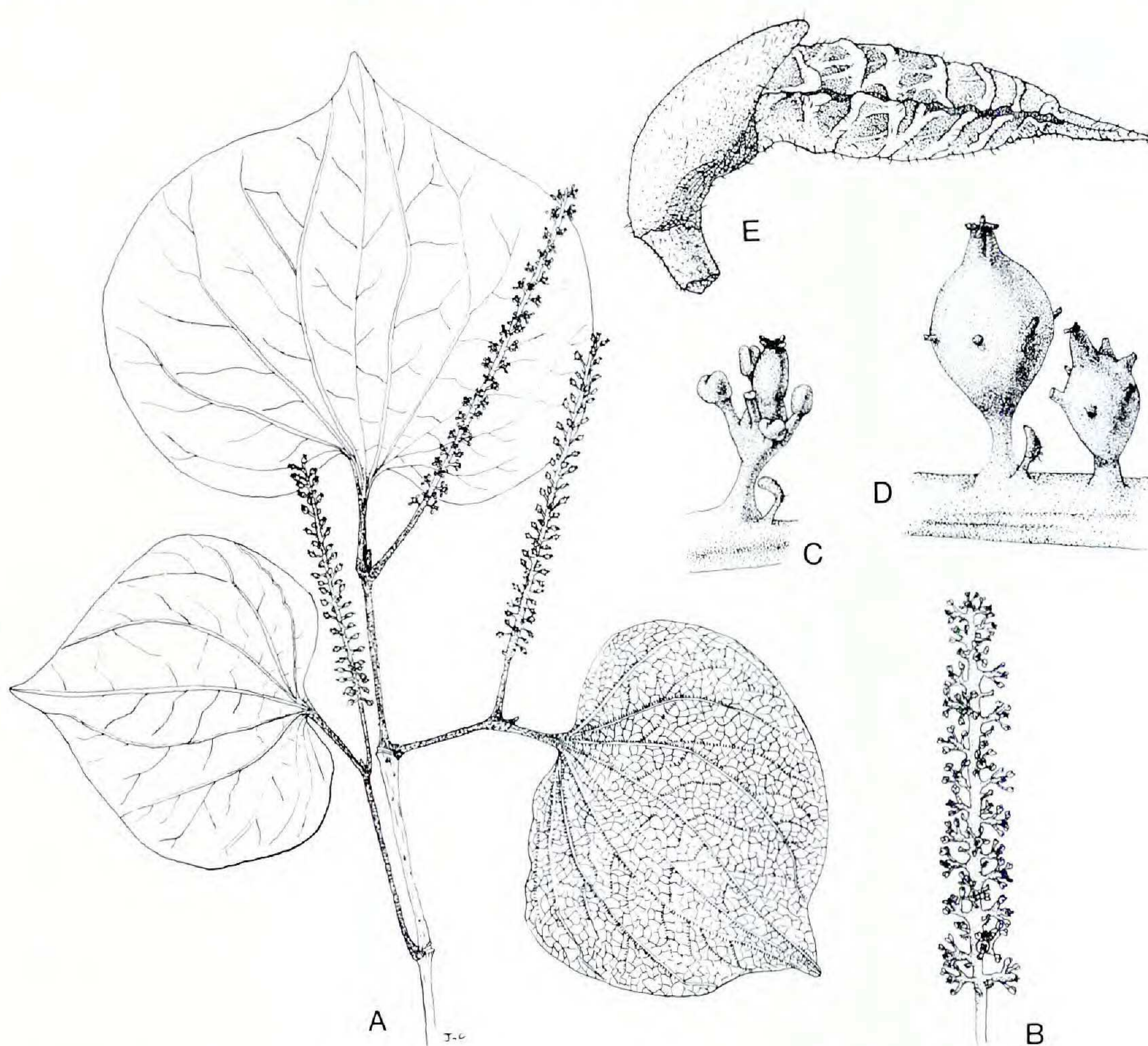


FIGURE 5. *Piper abalienatum*: A, flowering branch, $\times 0.2$; B, inflorescence, $\times 0.8$; C, flower with bract, $\times 12$; D, fruits with bract, $\times 5$; E, prophyll with emergent young leaf, $\times 3.5$.

Bornstein & Chase 94 (MICH); Coalcomán, *Hinton 13855* (ENCB, ILL, NA, NY, PH, TEX, US); 32 km N of Playa Azul (region of Los Encinos), *King & Soderstrom 4929* (NY, TEX, US).

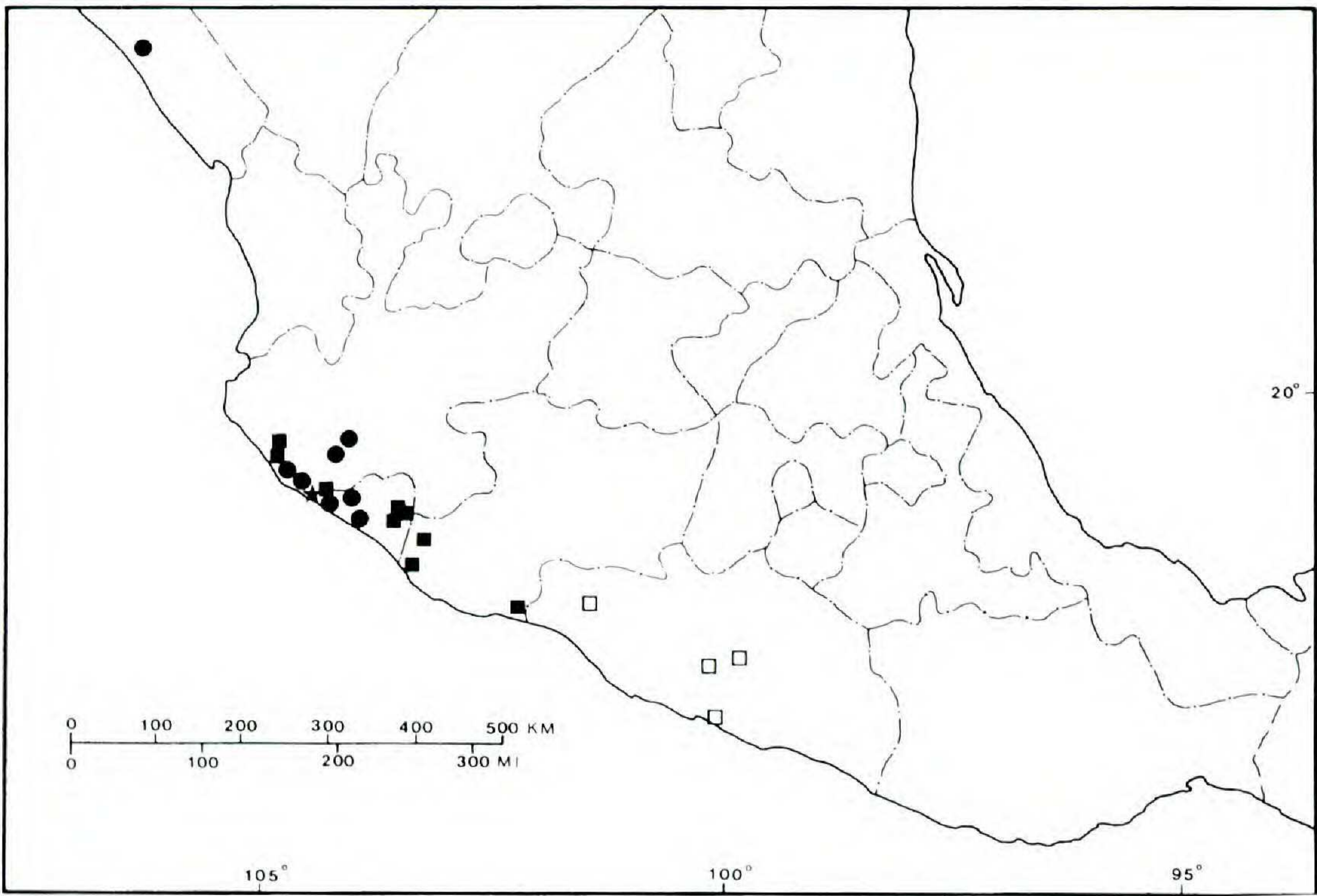
Piper abalienatum is most often confused with *P. stipulaceum*, because in both species the stamens are adnate to near the middle of the ovary. The differences between these two closely related taxa are discussed following the description of *P. stipulaceum* (and see TABLE).

Piper abalienatum also resembles *P. colotlipanense*, especially with respect to styler features and filament length. It is distinguished from that species in having the stamens adnate to the middle of the ovary (vs. hypogynous or irregularly adnate to the lower portion of the ovary).

2. ***Piper brachypus*** Trel. Amer. J. Bot. 8: 215. pl. 6. 1921. TYPE: Mexico, Colima, Manzanillo, 2–18 March 1891, *Palmer 1332* (holotype, US!; isotype, GH!).

FIGURE 6.

Shrub to 4 m tall; twigs and older branches glabrous to very sparsely puberulent with glandular hairs. Prophylls to 0.7 cm long, base truncate, apex



MAP 1. Distribution of *Piper abalienatum* (solid squares), *P. brevipedicellatum* (circles), *P. colotlipanense* (open squares), and *P. mcvaughii* (star).

Characters used to distinguish between *Piper abalienatum* and *Piper stipulaceum*.

CHARACTER	SPECIES	
	<i>Piper abalienatum</i>	<i>Piper stipulaceum</i>
Leaves		
Average size (cm)	12.6 × 11.8	10 × 8.7
Surface	Pubescent to tomentose, especially beneath	Puberulent to pubescent, especially beneath
Stamens		
Arrangement	Irregular; occasionally in 2 whorls	In 1 whorl
Filament length (mm)	0.5–1; equal to or exceeding anthers	To 0.5; shorter than or nearly equal to anthers
Ovary shape (in flower)	Ovoid-ellipsoid	Ovoid to globose
Style		
Shape	Columnar to slightly conical	Depressed-ovoid to conical
Length (mm)	(0.5–)1–1.5(–2)	To 0.5, rarely slightly longer
To ovary ratio		
In flower	ca. 1 : 1	1 : 1–1 : 3
In fruit	1 : 2–1 : 3	1 : 3–1 : 5

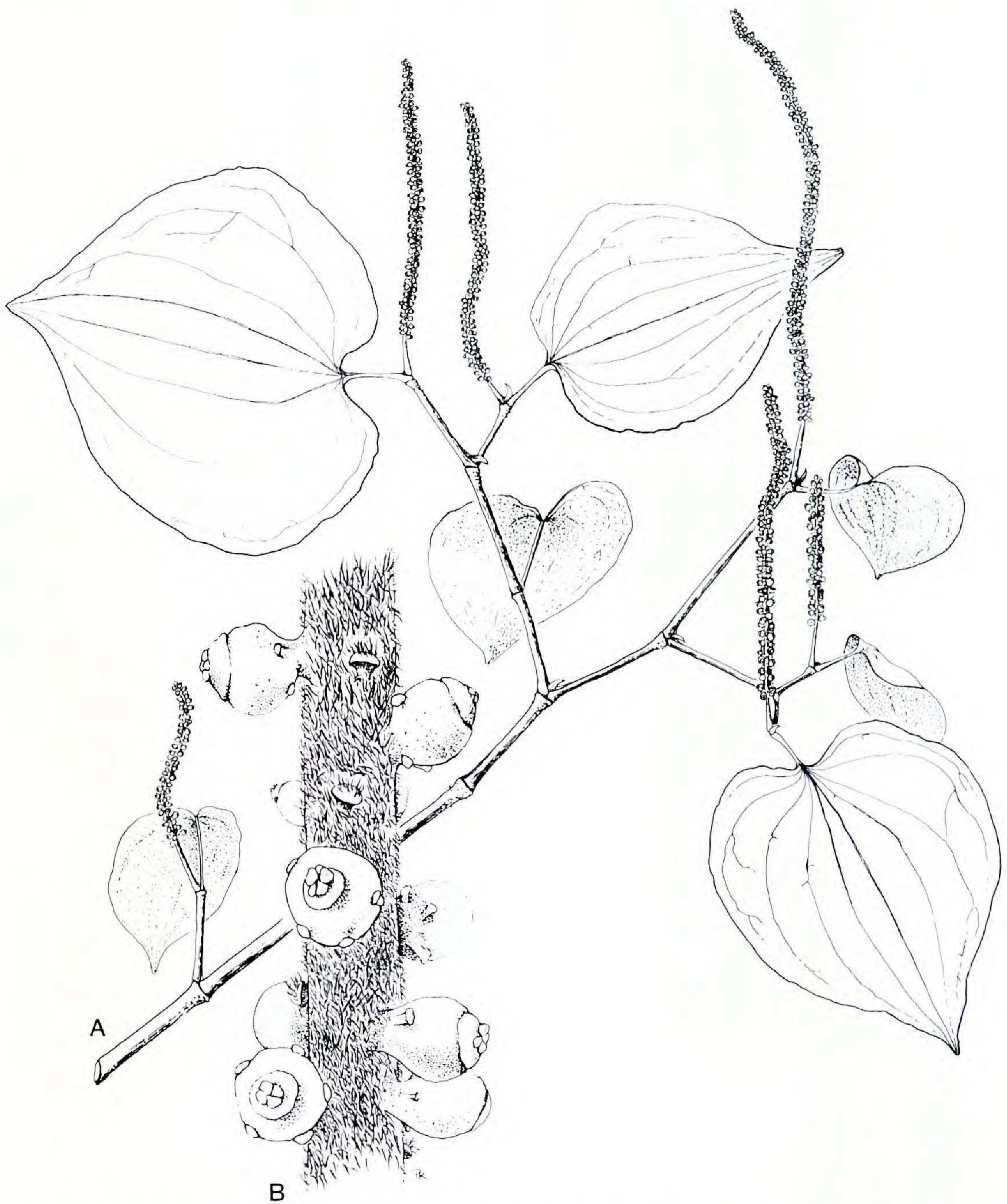
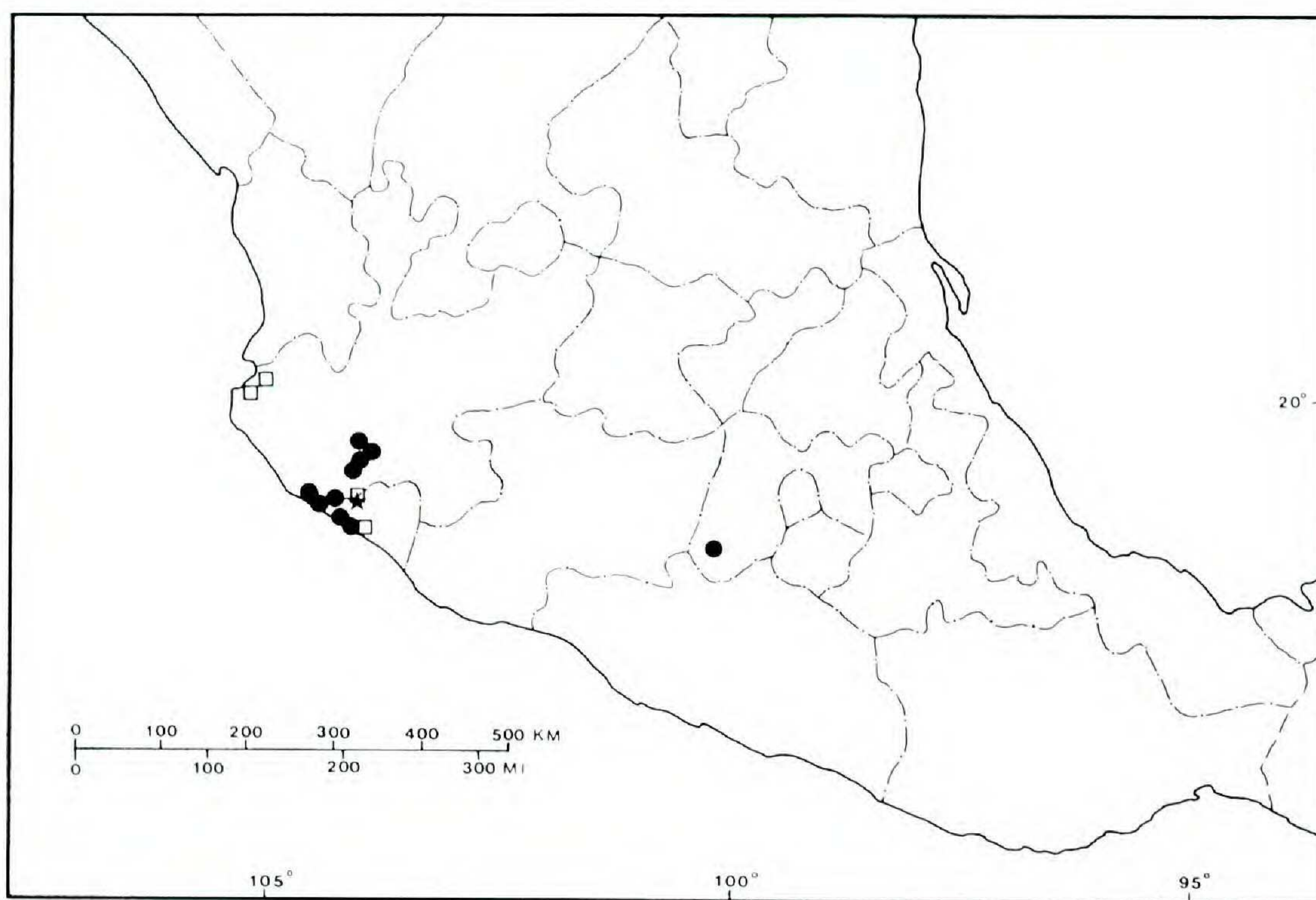


FIGURE 6. *Piper brachypus*: A, fruiting branch, $\times 0.4$; B, portion of infructescence, $\times 6$.

acute, glabrous or puberulent with short eglandular hairs. Leaves with petiole 0.7–1.6 cm long, narrow, glabrous or sparsely puberulent with glandular or short eglandular hairs; blade ovate to broadly ovate to occasionally suborbiculate, 4.4–8.6(–9.6) $\times$ 3.3–6.6(–9.1) cm, rounded to truncate to shallowly cordate at base, acuminate at apex, 5- to 7- (to 9-)nerved, glabrous to puberulent (especially at blade-petiole junction) with predominantly short eglandular hairs. Inflorescences (5.9–)6.8–11.6 cm long; peduncle glabrous to commonly puberulent to sparsely pubescent, remaining rachis pubescent to densely pubescent with long eglandular hairs; bracts sessile to subsessile, broadly spatulate to



MAP 2. Distribution of *Piper brachypus* (open squares), *P. cihuatlanense* (star), and *P. novogalicianum* (circles).

cupulate, to 0.5 mm long (rarely longer), pubescent to densely pubescent (especially abaxially) with eglandular hairs. Flowers with pedicel to 0.5(–1) mm long and in diameter, glabrous to puberulent with eglandular hairs; stamens 4 or 5 (or 6), hypogynous, to 1 mm long, the filaments to 0.5 mm long, the anthers small, dehiscing laterally; ovary ellipsoid to ovoid, puberulent with glandular hairs, the style depressed-ovoid to very short-conical, to 0.5 mm long, usually quite conspicuous in both flower and fruit, the stigma 3- to 5-lobed. Fruits ellipsoid to more commonly ovoid to globose, $1\text{--}1.75 \times 1\text{--}1.75$ mm, puberulent, style persistent but sometimes obscured by expanding ovary.

DISTRIBUTION. Growing in narrow band from Manzanillo, Colima, north to just south of Puerto Vallarta, Jalisco (see MAP 2).

HABITAT. Essentially unknown (*Mexia* and *Koelz* collections from wooded slopes, *Delgado et al.* from an oak forest). Near sea level to 450 m alt.

PHENOLOGY. Presumably follows phenological pattern of piper relatives in Nueva Galicia, therefore flowering May to July; specimens with fruits collected in March, mid to late July, November, and December.

SPECIMENS EXAMINED. **Mexico.** JALISCO: crossing puente of Río Las Juntas, on road to Puerto Vallarta, near El Tuito, *Delgado, Hernández, & Trejo* 204 (MICH); Quimixto, *Mexia* 1177 (A, GH, MO, NA, UC). COLIMA: vic. of Manzanillo, SW edge of Cuyutlán lagoon, *Ferris* 6186 (A); dry slope near Río Cihuatlán, N of Playa de Santiago, *Koelz* 34228 (ENCB, MICH).

Piper brachypus is distinguished by the combination of broadly ovate, glabrous leaves; pubescent rachises; densely pubescent bracts; subsessile flowers; hypogynous stamens; and small, usually ovoid to globose, conspicuously short-styled (= stylopodium, as described by Trelease) fruits.

3. ***Piper brevipedicellatum*** Bornstein, sp. nov.

FIGURE 7.

Frutex 2.5–5(–9) m altus, ramunculis pubescentibus; prophyllum 5–10(–13) mm longum, dorsaliter pubescens; folia laminis late ovatis vel orbiculatis, (6–)7.3–12.7 × (4.7–)5.6–12.8 cm, breviacuminatis vel acuminatis, basi cordatis, utrinque pubescentibus; inflorescentia 6–11.5(–13.4) cm longa, rhachidi puberula vel pubescenti pilis elongatis; bracteae usque ad 1 mm longae, spathulatae vel spathulicupulatae, abaxialiter pubescentes; pedicelli raro usque ad 1 mm longi; stamina hypogyna, ut videtur basi ovarii adnata, praecipue in fructu; stylus depresso-ovoideus vel breviconicus, usque ad 0.5 mm longus; fructus globosus, 2 × 2 mm, puberulus pilis glandulosis, stylo disciformi instructus.

TYPE. Mexico, Jalisco, 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, 250 m alt., 27 June 1983, *Bornstein & Weber-Bornstein 80* (holotype, MICH; isotypes, CHAP, GH, INIF, MEXU, NY).

Medium-sized treelike shrub, moderately branched from base, 2.5–5(–9) m tall; youngest twigs pubescent with eglandular hairs; older stems gray-brown with swollen nodes and warty lenticels, glabrous, maximum diameter to 5 cm. Prophylls 5–10(–13) mm long, base truncate, apex acute, abaxially puberulent to densely pubescent with eglandular hairs. Leaves with petiole 0.7–2.5 cm long, stout, puberulent to pubescent with eglandular hairs; blade broadly ovate to orbiculate, (6–)7.3–12.7 × (4.7–)5.6–12.8 cm, cordate at base, short-acuminate to acuminate at apex, 5- to 7-nerved, puberulent to more commonly pubescent above with predominantly eglandular hairs, pubescent beneath with both hair types (eglandular more abundant and conspicuous on major veins, glandular more predominant in areolar regions). Inflorescences 6–11.5(–13.4) cm long, green becoming yellow-white to white; peduncle stout, puberulent to pubescent with eglandular hairs, remaining rachis sparsely puberulent or subglabrous to pubescent with eglandular hairs; bracts to 1 mm long, sessile or subsessile, broadly spatulate to broadly spatulate-cupulate, 0.5–1 mm long, sparsely pubescent to pubescent with eglandular hairs abaxially, occasionally with some pubescence adaxially. Flowers with pedicel rarely to 1 mm long and wide, glabrous to puberulent with glandular and eglandular hairs; stamens 4 to 6 (or 7), hypogynous although often (especially in fruit) appearing as if adnate to base of ovary, filaments and anthers ± equal in length, anthers occasionally dehiscing slightly upward from lateral; ovary ovoid to globose, puberulent with glandular hairs, the style depressed-ovoid to short-conical, to 0.5 mm long, persistent in fruit, the stigma 3- to 5-lobed. Fruits globose at maturity, to 2 mm in diameter, puberulent.

DISTRIBUTION. Central Colima north to southwestern Jalisco from near sea level to ca. 1200 m alt. (see MAP 1). Also known from a single disjunct collection

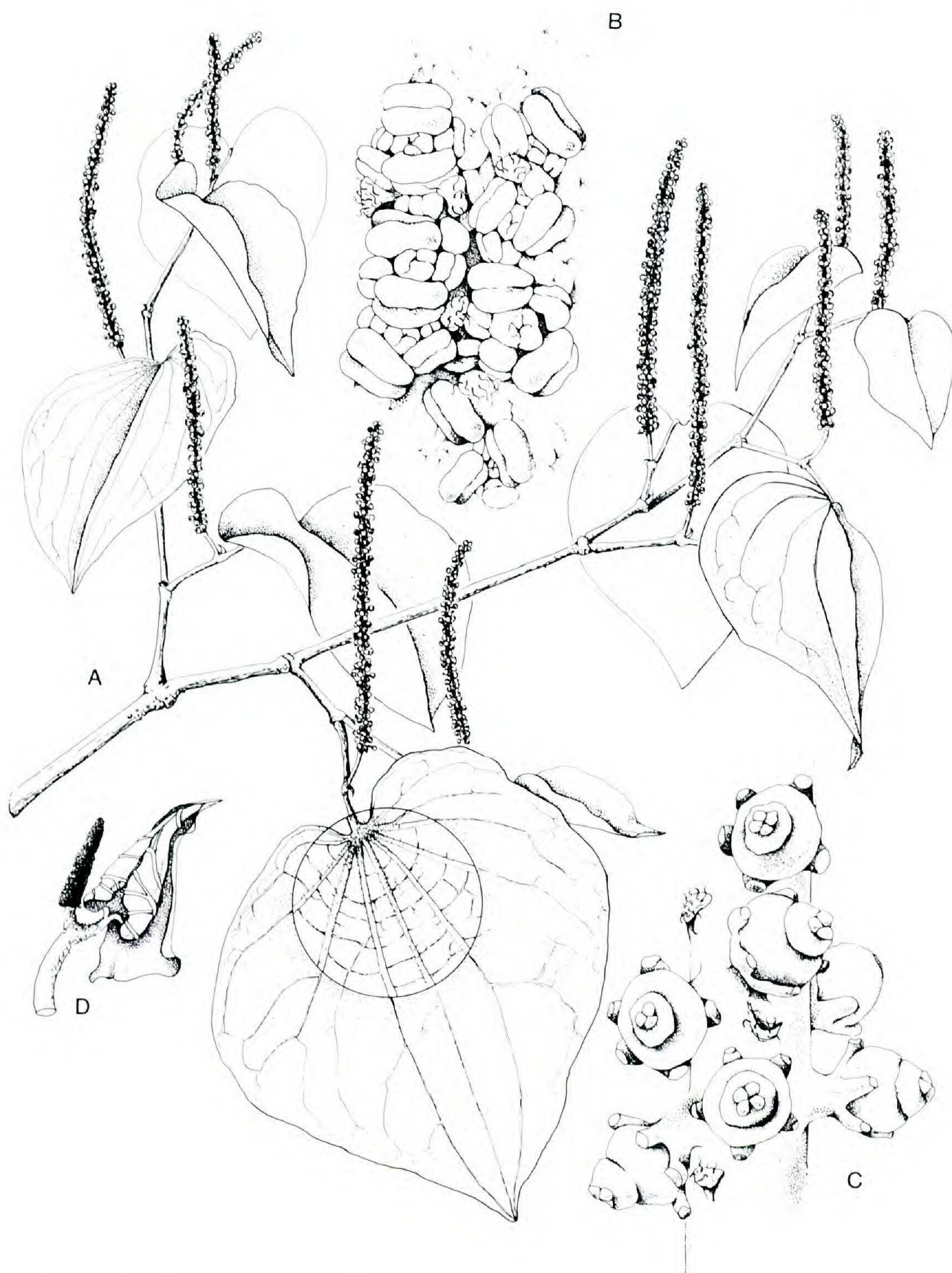


FIGURE 7. *Piper brevipedicellatum*: A, fruiting branch, $\times 0.4$, with detailed inset of petiole-blade junction showing indument; B, portion of young inflorescence, $\times 5.6$; C, portion of infructescence, $\times 5.6$; D, prophyll with emergent young leaf and inflorescence, $\times 1.9$.

ca. 500 km north in Sinaloa, which represents the northernmost extent of subg. *Arctottonia*.

HABITAT. Tolerant of a variety of conditions, including shaded, low-elevation palm forests dominated by *Orbignya cohune*, deciduous to subdeciduous, low-

elevation forests near intermittent mountain streams, and deciduous, mid-elevation forests probably dominated by *Quercus* spp. The only potential common denominator of these sites is disturbance, which indicates that this species colonizes second-growth forests.

PHENOLOGY. Flowering late May through June and possibly early July. Fruits appear in late June; collected as late as December.

SPECIMENS EXAMINED. **Mexico.** SINALOA: Sierra de Pinal, just E of El Espinal, *Kimnach & Mejorada* 2266 (MEXU, US). JALISCO: along Hwy. 80 between Autlán and Melaque, 4 km N of side road to Casimir Castillo, *Bornstein* 75 (MICH); 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, *Bornstein & Weber-Bornstein* 81 (MICH); 0.9 km de la carretera Puerto Vallarta–Barra de Navidad, ca. 7 km al SE de la Estación de Biología Chamela, sobre el camino a “El 25” (IMSS comunidad), *Lott & Magallanes* 611 (MICH); Estación de Biología, Los Pozos, Arroyo Colorado, *Lott* 719 (MICH); ca. 8 mi S of Autlán toward La Resolana, *Wilbur* 1625 (MICH). COLIMA: 0.5 km S of Comatlán on Hwy. 98 to Minatitlán, *Bornstein* 87 (MICH); ca. 16 mi WNW of Santiago, road to Cihuatlán, *McVaugh* 14983 (MICH); km 293, ca. 15 mi SE of Manzanillo, *McVaugh & Koelz* 1623 (MICH).

Piper brevipedicellatum and *P. brachypus* both have flowers with hypogynous stamens and fruits crowned by a “stylopodial disk.” However, in the former species there is a strong tendency toward adnation of the stamens to the ovary and the rachis appears less pubescent than in *P. brachypus*. Unfortunately, neither of these features is consistently different. On the other hand, the two species are quite distinct vegetatively since *P. brachypus* is essentially glabrous, whereas *P. brevipedicellatum* has pubescent twigs, prophylls, and leaves.

4. *Piper cihuatlanense* Bornstein, sp. nov.

FIGURE 8.

Frutex usque ad 6 m altus, ramunculis et ramis glabris; prophyllum usque ad 6 mm longum, glabrum vel puberulum; folia laminis ellipticis vel anguste ovatis, $4.9\text{--}7.3 \times 2.7\text{--}3.9$ cm, acuminatis, basi rotundatis, glabris vel sparsim puberulis; inflorescentia 6.5–9.1 cm longa, rhachidi dense pubescenti pilis eglandulatis longis; bracteae 0.25–0.5 mm longae, spathulatae vel cupulatae, dense pubescentes pilis eglandulatis longissimis; pedicelli (0.5–)1(–1.5) mm longi, pubescentes; stamina hypogyna; stylus usque ad 0.25 mm longus, depresso-ovoideus, inconspicuus; ovarium et fructus ellipsoideus vel obovoideus vel globosus, $1\text{--}1.5 \times 0.75\text{--}1.25$ mm, puberulus.

TYPE. Mexico, Colima, steep, heavily wooded, moist ravines in gorge of Río Cihuatlán, near bridge 13 mi N of Santiago, 200–300 m alt., 27 July 1957, *McVaugh* 15838 (holotype, MICH).

Treelike shrub to 6 m tall; twigs and older branches brown (occasionally silvery due to detaching epidermis), glabrous or with few locally concentrated eglandular hairs, especially at branch points, with inconspicuous round, pale brown lenticels. Prophylls to 0.6 cm long, base unknown, apex acute, glabrous to puberulent with very short eglandular hairs. Leaves with petiole 0.4–1.1 cm long, appearing glabrous but usually sparsely puberulent with glandular or very short eglandular hairs; blade elliptic to narrowly ovate, $4.9\text{--}7.3 \times 2.7\text{--}3.9$ cm, round at base, acuminate at apex, 5-nerved, glabrous to sparsely puberulent

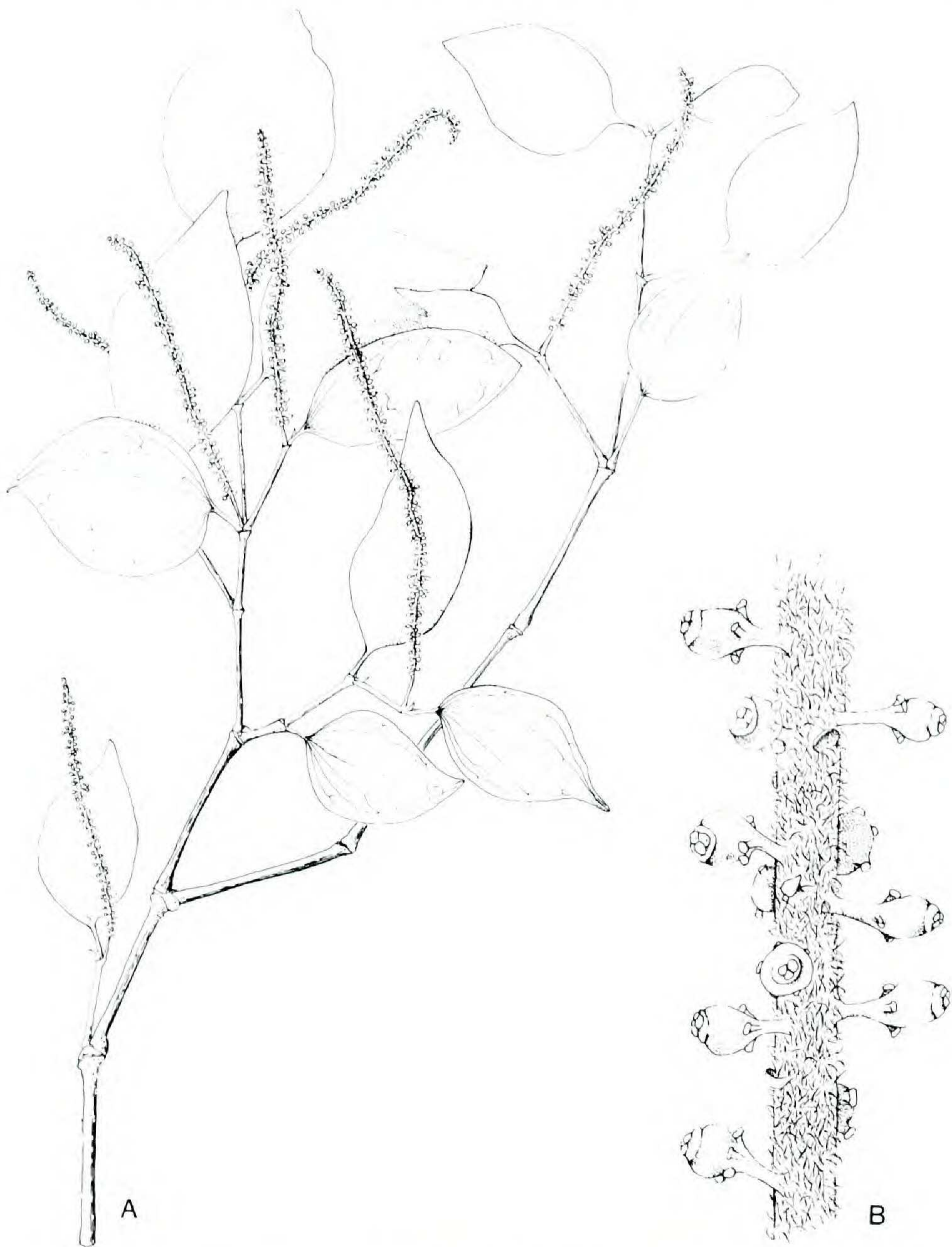


FIGURE 8. *Piper cihuatlanense*: A, fruiting branch, $\times 0.45$; B, portion of infructescence, $\times 6.8$.

(especially at blade-petiole junction) with short eglandular hairs. Inflorescences drooping, 6.5–9.1 cm long, color unknown; peduncle puberulent, passing abruptly into rachis, this densely pubescent with elongate eglandular hairs; bracts broadly spatulate to cupulate, < 0.5 mm long, usually ca. 0.25 mm, densely pubescent with very long eglandular hairs on both surfaces. Flowers with pedicel (0.5–) 1(–1.5) mm long, narrow, usually 1.5–2 times as long as broad, puberulent to distinctly pubescent with eglandular hairs; stamens 4 to 6, hypogynous, the filaments < 0.25 mm long, the anthers subglobose, to 0.5 mm long, dehiscing laterally; ovary ellipsoid to obovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid, < 0.25 mm long, inconspicuous in flower,

totally obscured in fruit, the stigma 3- or 4- (or 5-)lobed. Fruits similar to ovary in shape, $1-1.5 \times 0.75-1.25$ mm, puberulent.

DISTRIBUTION. Known from two localities in northwestern Colima (see MAP 2).

HABITAT. Apparently restricted to barrancas of Río Cihuatlán at 200–300 m alt. (This area is quite moist during the rainy season and supports a dense tropical subdeciduous vegetation.)

PHENOLOGY. The McVaugh and Koelz collections suggest a flowering period that lasts through the rainy season (mid-May through October). More direct evidence is needed.

SPECIMENS EXAMINED. **Mexico.** COLIMA: barranca of Río Cihuatlán, N of Playa Santiago, Koelz 34223 (ENCB, MICH).

Piper cihuatlanense is easily distinguished by its small, elliptic to narrowly ovate, subglabrous leaves, its very densely pubescent rachis and bracts with relatively long eglandular hairs, its often-pubescent pedicels, and its virtually nonexistent style (especially in fruit). If it is true that the racemes droop, as is indicated on the label of the type specimen, then this would also be a unique feature (for the entire subgenus).

5. *Piper colotlipanense* Bornstein, sp. nov.

FIGURE 9.

Frutex usque ad 2.1 m altus, ramunculis fulvis dense tomentosis; prophyllum usque ad 0.8 cm longum, dorsaliter dense pubescens vel tomentosum; folia laminis late ovatis vel fere orbiculatis, $(5.3-6.6-13.1 \times 4.6-11.6)$ cm, brev-acuminatis vel acuminatis, basi rotundatis vel leviter cordatis, supra pubescentibus, subter pubescentibus vel tomentosis; inflorescentia 8.1–10.1 cm longa, rhachidi pubescenti vel sparsim pubescenti; bracteae 0.5–1 mm longae, spathulatae vel spathulicupulatae et breviter vel longe petiolatae, pubescentes vel dense pubescentes; pedicelli $(0.5-1.5(-2.5))$ mm longi; stamina hypogyna filamentis elongatis, 0.5–1 mm longis; stylus depresso-ovoideus vel conicus; ovarium et fructus ovoideus vel globosus, puberulus.

TYPE. Mexico, Guerrero, 2 mi W of Colotlipa, 2700 ft alt., 22 June 1953, Rowell & Kubicek 3666 (holotype, MICH).

Medium-sized treelike shrub to 2.1 m tall; youngest twigs densely tawny-tomentose with eglandular hairs, becoming silvery and glabrous; older stems drying brown to gray, with swollen nodes and warty lenticels. Prophylls to 0.8 cm long, base truncate, apex acute, abaxially densely pubescent to tomentose with eglandular hairs. Leaves with petiole 1.1–2.3 cm long, narrow, vaginate at base or occasionally for nearly $\frac{1}{2}$ length of petiole, densely soft-pubescent to tomentose with eglandular hairs; blade broadly ovate to nearly orbiculate, $(5.3-6.6-13.1 \times 4.6-11.6)$ cm, rounded to shallowly cordate at base, short-acuminate to acuminate at apex, 5- to 7- (to 9-)nerved, pubescent above (especially along major veins), densely pubescent to tomentose beneath (especially along major veins), the hairs long, eglandular. Inflorescences 8.1–10.1 cm long, color unknown; peduncle pubescent to tomentose at base with eglandular hairs,

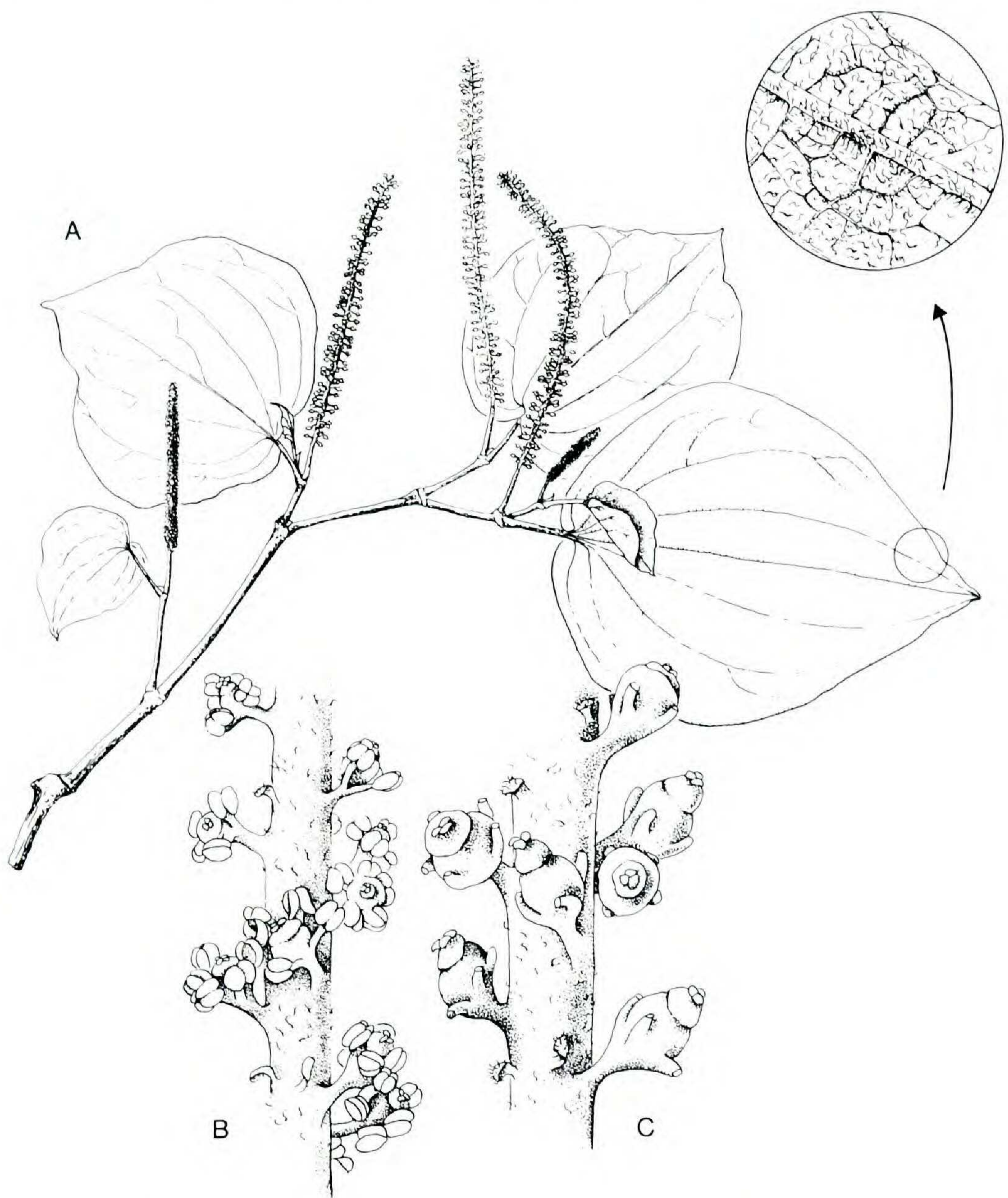


FIGURE 9. *Piper colotlipanense*: A, flowering branch, $\times 0.42$, with detailed inset of lower leaf surface showing indument; B, portion of inflorescence, $\times 6.3$; C, portion of semimature infructescence, $\times 6.3$.

gradually transitional to sparsely pubescent for remaining rachis; bracts sessile or subsessile to distinctly long-petiolate, spatulate to spatulate-cupulate at apex, 0.5–1 mm long, pubescent to densely pubescent with eglandular hairs, most often on abaxial surface. Flowers with pedicel (0.5–)1.5(–2.5) mm long, up to 0.5 mm in diameter, glabrous to puberulent with glandular hairs, occasionally sparsely pubescent with eglandular hairs; stamens (4 or) 5 or 6, hypogynous, the filaments 0.5–1 mm long, the anthers to 0.5 mm long, rarely slightly longer, dehiscing laterally to slightly divergent upward from lateral; ovary ovoid to globose, puberulent with glandular hairs, the style depressed-ovoid to conical,

in young fruit $\frac{1}{3}$ – $\frac{3}{4}$ length of ovary, the stigma 3- or 4-lobed. Fruits (when submature) ovoid to globose, style very evident.

DISTRIBUTION. Guerrero, in low mountains of Sierra Madre del Sur, south of Chilpancingo de los Bravos (see MAP 1).

HABITAT. Herbarium label data indicate that this species occurs near edges of streams or rivers, or on hillsides on rocky soil at 150–850 m alt.

PHENOLOGY. Flowering May through June, possibly into early July. Young fruits in early June, expected into July and August.

REPRESENTATIVE SPECIMENS. **Mexico.** GUERRERO: S of Chilpancingo, *Clark 7141* (MO, NY); Vallecitos, Montes de Oca, *Hinton 10261* (ILL, K, NA, NY, PH, TEX, US); Pie de la Cuesta, 10 mi N of Acapulco, *MacDaniels 201* (F); 1 mi W of Achuitzotla, *Rowell & E. H. Cooper 2507* (MICH); 1 mi W of Colotlipa, *Rowell & Irby 3523* (MICH). LOCALITY UNKNOWN: *Sessé & Mociño 318* (F), *328* (F), *329* (F), *339* (ILL), *348* (F, ILL).

Piper colotlipanense is distinguished by its densely long-pubescent prophylls and leaves and its hypogynous stamens with long filaments.

6. ***Piper guazacapanense*** Trel. & Standley, *Fieldiana, Bot.* **24**: 301. 1952. TYPE: Guatemala, Santa Rosa, along Avellana road, S of Guazacapán, 150 m alt., 12 June 1940, *Standley 79461* (holotype, F!; isotype, NY!).

FIGURE 10.

Procumbent perennial, occasionally rooting at nodes; stems largely herbaceous, becoming woody with age, glabrous. Prophylls to 8 mm long, base truncate, apex acute, abaxially puberulent to hirtellous. Leaves with petiole 4–17 mm long, slender, hirtellous with both glandular and eglandular hairs; blade broadly ovate to orbiculate-ovate, (3.5–)5–9 × 4–8 cm, cordate with rounded lobes at base, gradually to abruptly acuminate or long-acuminate at apex, 5-nerved (3 principal veins persistent almost to apex), dark green above and sparsely puberulent, paler beneath and puberulent to hirtellous with eglandular hairs ± restricted to veins and glandular ones to areoles. Inflorescences 1–3 (–4.2) cm long, yellow-green when young, turning white at maturity; peduncle and rachis glabrous to more commonly puberulent; bracts spatulate-cupulate to broadly cupulate, rarely to 1 mm long, abaxially puberulent with eglandular hairs (rarely glabrous). Flowers with pedicels 1–2.5 mm long, glabrous or occasionally minutely puberulent; stamens 4 to 7, hypogynous, filaments 0.25 mm long, anthers dehiscing laterally; ovary ovoid to globose, minutely puberulent with glandular hairs, the style $\frac{1}{2}$ to equal the ovary in length, becoming obliterated in fruit, the stigma 3- or 4-lobed. Fruits globose, 2–2.5 mm in diameter, green when young, translucent pearl white at maturity, puberulent.

DISTRIBUTION. Southwestern Chiapas on northwestern edge of Sierra Madre de Chiapas, the north-central plateau in Chiapas, and southeastern Guatemala on southern edge of Sierra Madre (see MAP 3).

HABITAT. Moist, shaded ravines. Commonly found as dense groundcover along banks above small streams in tropical subdeciduous forests at 150–1000 m alt.

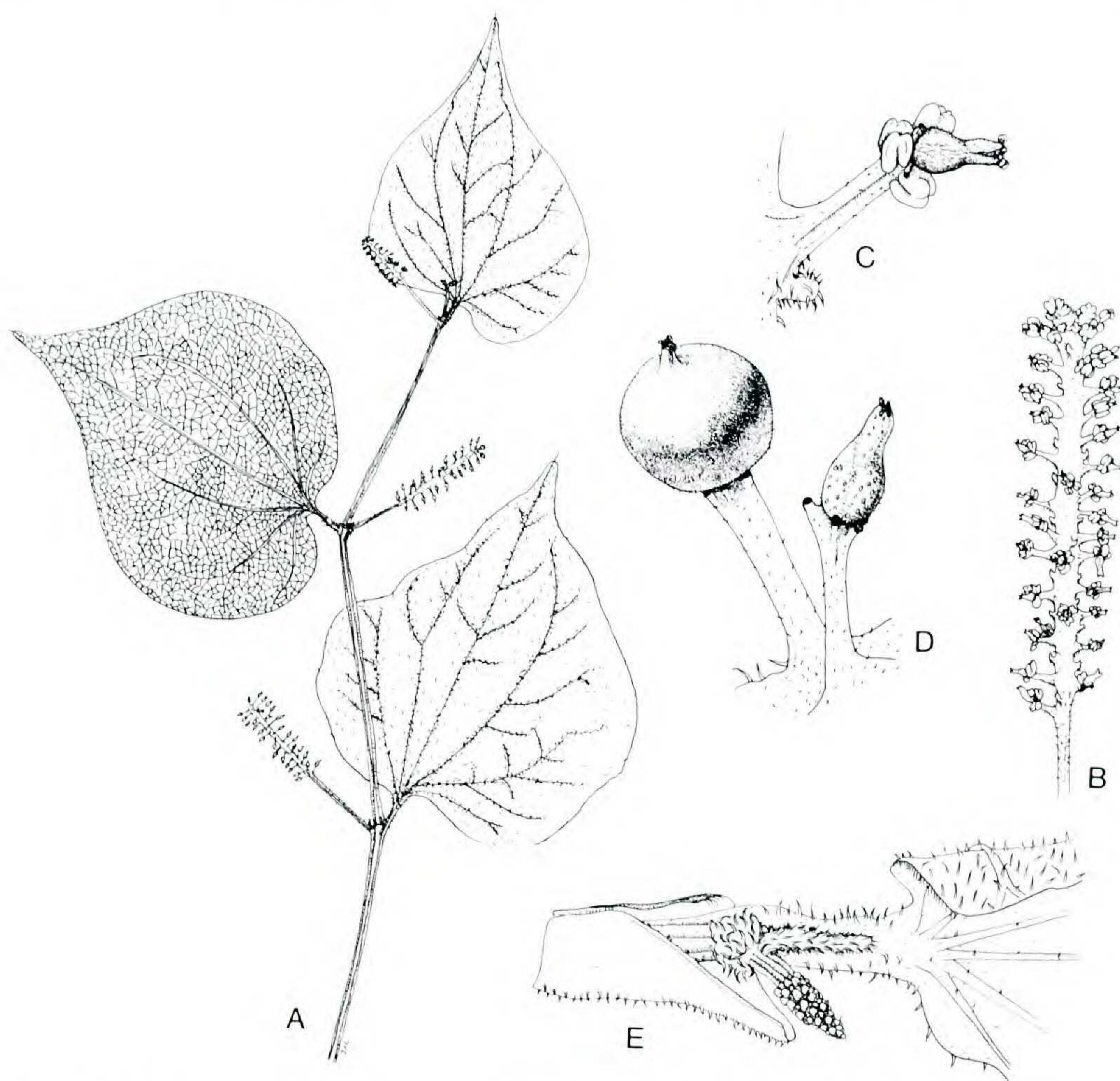


FIGURE 10. *Piper guazacapanense*: A, flowering branch, $\times 0.4$; B, inflorescence, $\times 1.6$; C, flower with bract, $\times 13$; D, immature and mature fruits, $\times 8.6$; E, prophyll with young leaf, young inflorescence, and succeeding prophyll, $\times 13$.

PHENOLOGY. Flowering mid-February to late May or early June, predominantly in April and May. Fruits collected in October, December, and February.

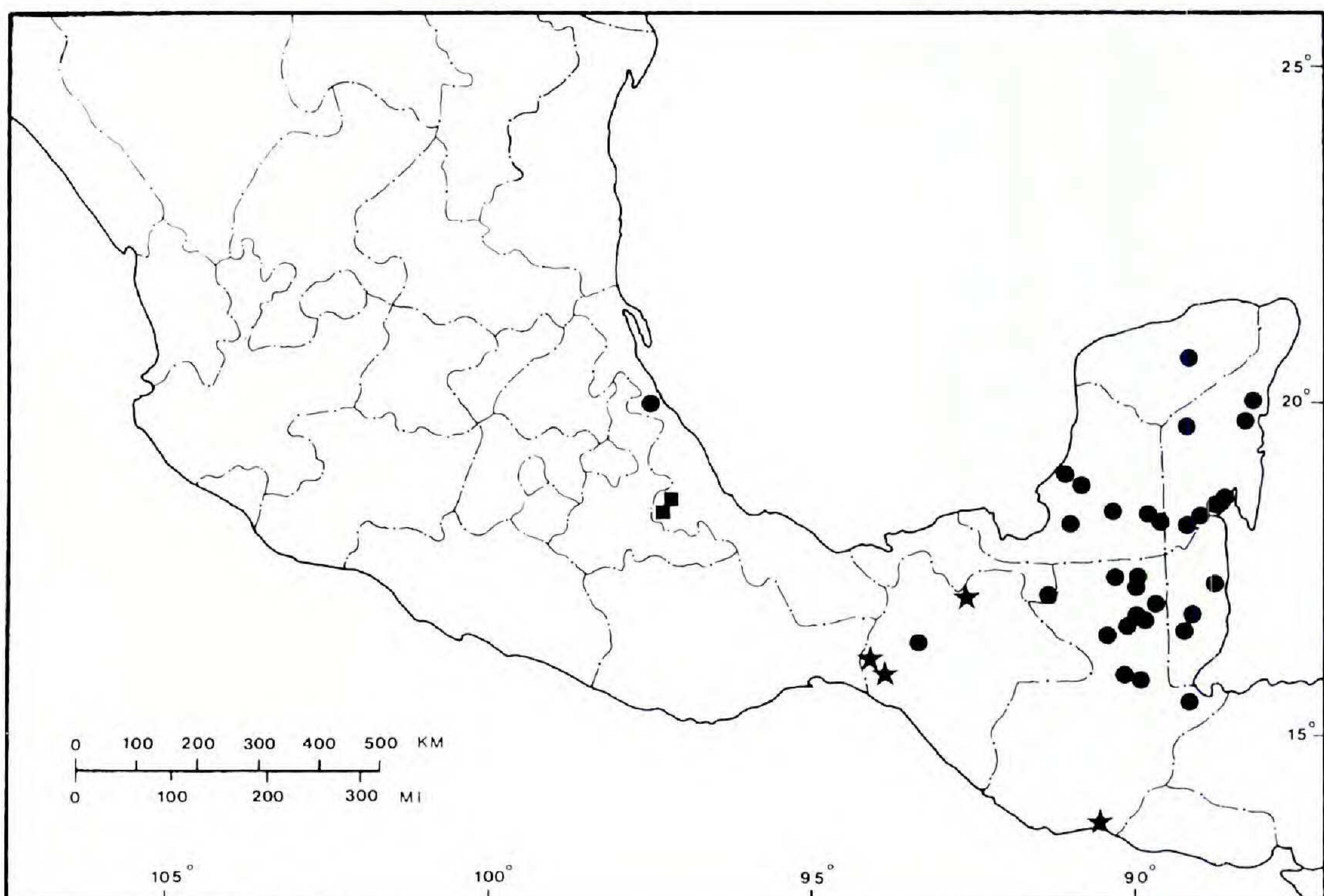
REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: 12 km S of Hwy. 190 near Rizo de Oro, behind microwave tower of La Mina in moist shaded ravine, *Bornstein, Chase, & Bornstein* 59 (MICH); 13 mi N of Arriaga along Hwy. 195 on steep slopes along ravines, *Breedlove* 25520 (ENCB, F, MEXU, MICH, MO, NY, TEX); along river below Huitiupan, *Breedlove & A. C. Smith* 32576 (MEXU).

Piper guazacapanense is easily recognized by its prostrate habit, its small, heart-shaped leaves, its short, few-flowered inflorescences, and its globose, translucent fruits.

7. *Piper mcvaughii* Bornstein, sp. nov.

FIGURE 11.

Frutex ramunculis fere glabris; prophyllum usque ad 0.3 cm longum, puberulum vel brevipubescens; folia laminis late ovatis, 5.1–8 $\times$ 5.5–7.6 cm, breviacuminatis, basi cordatis, supra puberulis, subter sparsim puberulis; in-



MAP 3. Distribution of *Piper guazacapanense* (stars), *P. muelleri* (squares), and *P. neesianum* (circles).

florescentia 6.7–8.8 cm longa, rhachidi sparsim puberula pilis glandulosis; bracteae usque ad 0.75 mm longae, late spathulatae vel valde cupulatae, sparsim puberulae vel puberulae; pedicelli 0.5(–0.75) mm longi, sparsim pubuleri, pilis glandulosis; stamina ovario adnata; stylus depresso-ovoideus vel brevicolumnaris, usque ad 0.75 mm longus; ovarium ovoideum-ellipsoideum; fructus globosus, usque ad 2 mm diametro, puberulus.

TYPE. Mexico, Jalisco, coastal plain near hwy. to Autlán, 4 mi N of Bahía Navidad, 40 m alt., 8 Nov. 1960, *McVaugh 20817* (holotype, MICH).

Shrub of unknown dimensions; youngest twigs drying brown, with sparse glandular hairs; older branches silvery, with brown, warty lenticels, glabrous. Prophylls to 3 mm long, base truncate, apex acute, abaxially puberulent to short-pubescent with glandular or short eglandular hairs. Leaves with petiole 1.1–1.8 cm long, narrow, appearing glabrous but sparsely puberulent with glandular hairs; blade broadly ovate, 5.1–8 × 5.5–7.6 cm, cordate at base, short-acuminate at apex, 5- (to 7-)nerved, puberulent above with predominantly glandular hairs (especially at petiole-blade junction and along blade margin), sparsely puberulent beneath on major veins, with mostly short eglandular hairs. Inflorescences 6.7–8.8 cm long, color unknown, with flowers widely spaced at maturity; peduncle and rachis sparsely puberulent with glandular hairs; bracts sessile or subsessile, broadly spatulate to occasionally strongly cupulate, to 0.75 mm long, sparsely puberulent to puberulent with glandular or short eglandular hairs. Flowers with pedicel ca. 0.5(–0.75) mm long and broad, sparsely puberulent with glandular hairs; stamens 4 or 5, adnate from

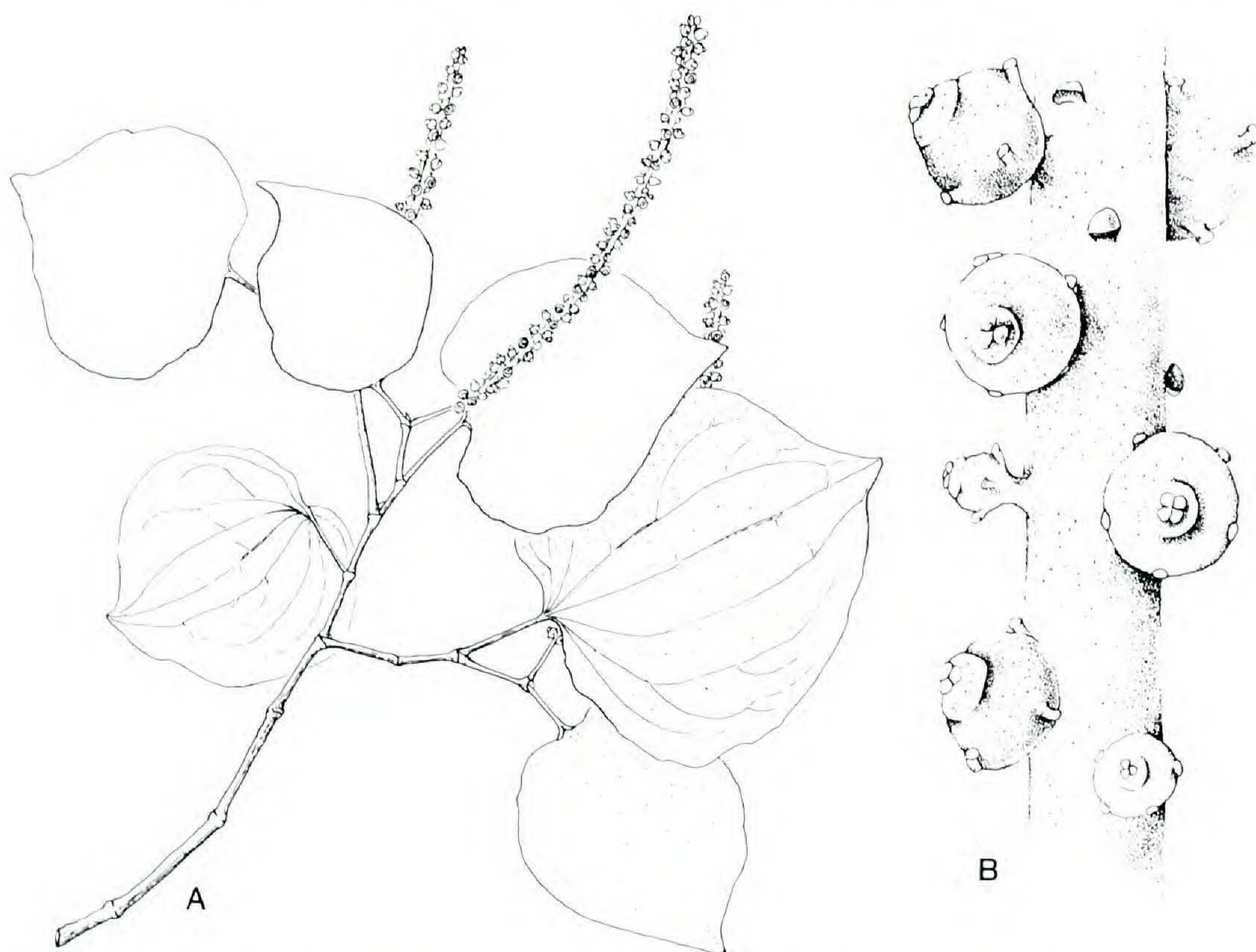


FIGURE 11. *Piper mcvaughii*: A, fruiting branch, $\times 0.4$; B, portion of infructescence, $\times 6$.

near base to middle of ovary, filaments ca. 0.25–0.5 mm long, anthers unknown; ovary ovoid-ellipsoid in late flower–early fruit, puberulent with glandular hairs, the style depressed-ovoid to short-columnar, to 0.75 mm long, the stigma (3- or) 4- or 5-lobed. Fruits globose at maturity, 2 mm in diameter, puberulent, style persistent and conspicuous.

DISTRIBUTION. Known only from type locality, southwestern Jalisco near Colima border (see MAP 1).

HABITAT. Type collection from second-growth deciduous forest with associated species of *Cordia* L., *Trichilia* P. Browne, and *Sideroxylon* L.

PHENOLOGY. Relatively unknown. Holotype, collected in November, has predominantly mature fruits. Based on flowering times of neighboring pipers, this species probably flowers from late May through June, at the beginning of the rainy season.

EPONYMY. Named in honor of Rogers McVaugh, Professor Emeritus at the University of Michigan, for his contributions that have increased our knowledge of botany in Mexico, and especially for his work on the flora of Nueva Galicia.

Superficially similar to *Piper brachypus*, *P. mcvaughii* differs in having stamens adnate to the ovary (vs. hypogynous) and the rachis and bracts puberulent

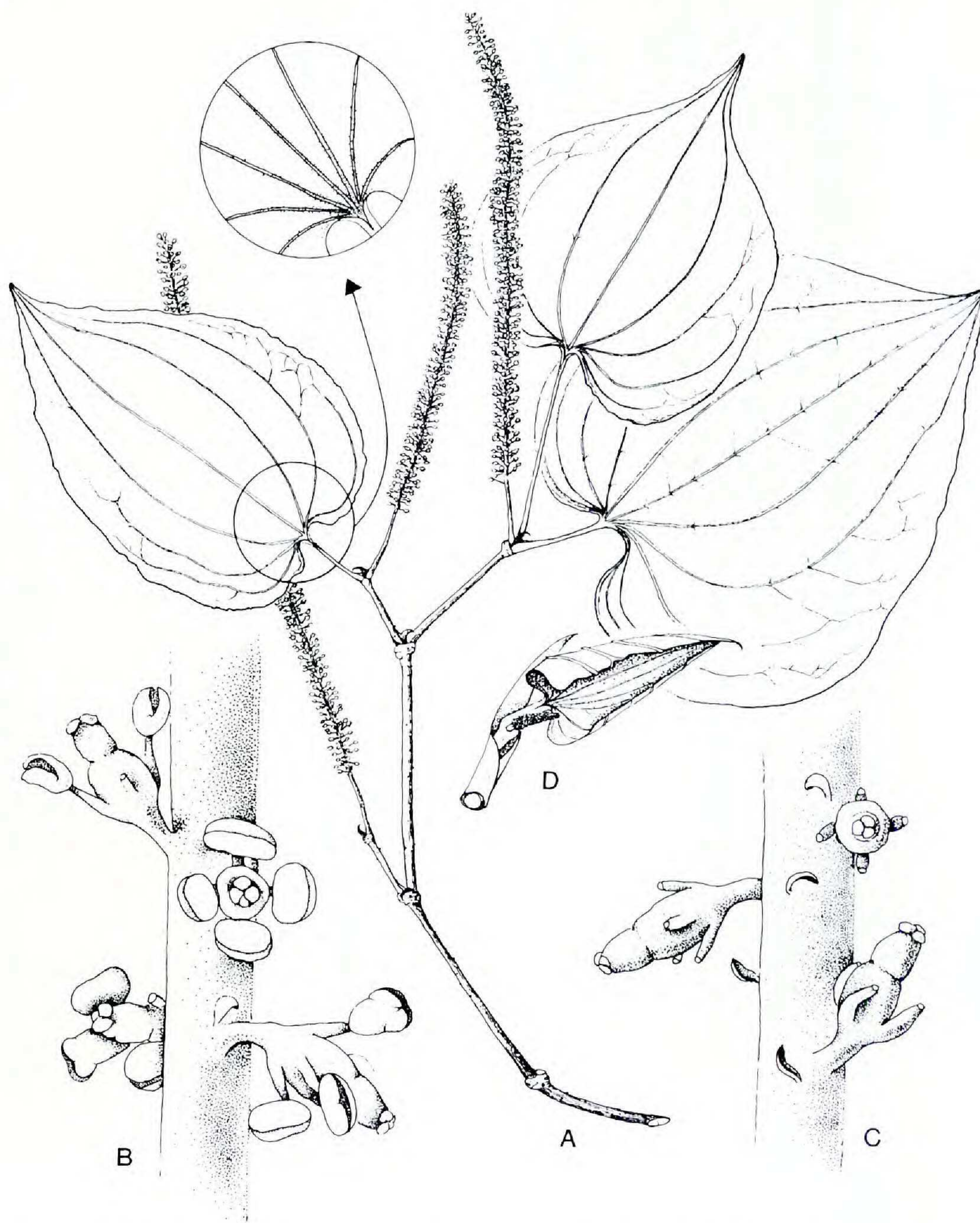


FIGURE 12. *Piper michelianum*: A, flowering branch, $\times 0.42$, with detailed inset of petiole-blade junction to show puberulence; B, portion of inflorescence in late flower-early fruit, $\times 6.3$; C, portion of young infructescence, $\times 6.3$; D, prophyll with emergent young leaf and inflorescence, $\times 2.1$.

with predominantly glandular hairs (vs. pubescent to densely pubescent with eglandular ones).

8. ***Piper michelianum*** C. DC. *Annuaire Conserv. Jard. Bot. Genève* **21**: 317. 1920. TYPE: Mexico, Michoacán, El Muleto, 850 m alt., 30 June 1898, *Langlassé 215* (holotype, G!; isotypes, GH!, K!, US!). FIGURE 12.

Piper mas Trel. *Amer. J. Bot.* **8**: 215. *pl. 7, fig. 2*. 1921. TYPE: Mexico, Michoacán, El Muleto, 850 m alt., 30 June 1898, *Langlassé 215* (holotype, US!; isotypes, G!, GH!, K!).

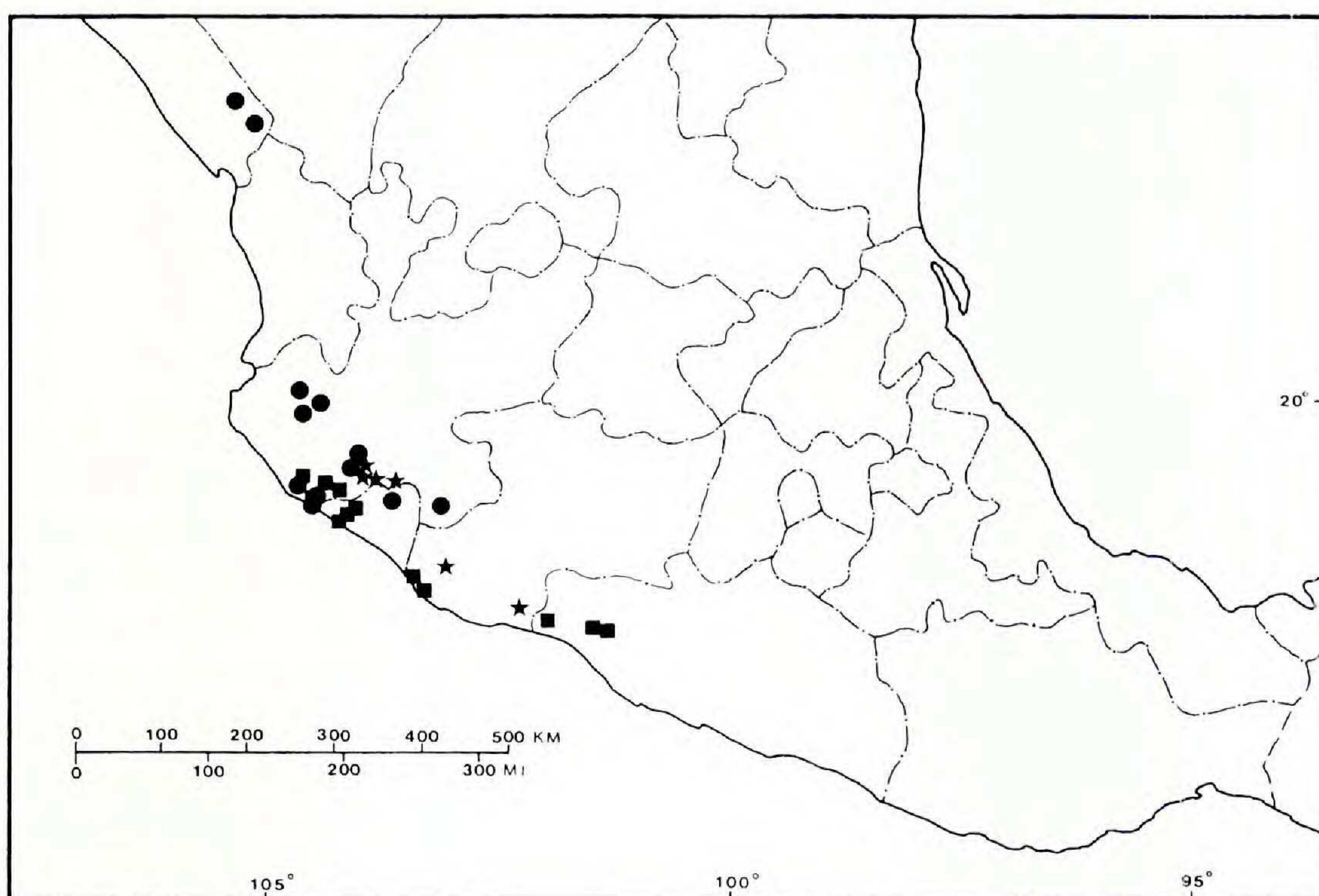
Medium-sized shrub, sparsely branched from base, appearing treelike, 2–5 m tall; youngest twigs very minutely and sparsely puberulent, predominantly with glandular hairs, soon glabrescent; older branches brownish, with warty lenticels; stems ash-gray, with swollen nodes, maximum diameter 6 cm. Prophylls to 1.2 cm long, base truncate, apex narrow and acuminate, both surfaces glabrous. Leaves with petiole 0.9–2 cm long, narrow, glabrous to puberulent (especially near blade junction) with eglandular hairs; blade round-ovate, (6–) 7.2–10.9(–13.4) × 6.1–8.6(–12.3) cm, shallow to moderately cordate at base, acuminate at apex, (5- to) 7-nerved, puberulent above with glandular and eglandular hairs (the latter generally restricted to veins), puberulent to sparsely and transiently pubescent beneath (especially on proximal ½) with glandular and eglandular hairs. Inflorescences 8.5–15.7 cm long, greenish when young, cream colored and fragrant at maturity; peduncle stout, glabrous to very minutely puberulent with mostly glandular hairs, remaining rachis glabrous to puberulent with glandular or very short eglandular hairs; bracts variable, ranging from sessile and strongly cupulate to distinctly petiolate with petiole gradually to abruptly expanding into spatulate to spatulate-cupulate apex, 0.25–1 mm long, abaxially glabrous to puberulent to very sparsely pubescent with eglandular hairs. Flowers with pedicel 0.5–2.5 mm long (depending on maturity), rarely to 0.5 mm wide, glabrous to puberulent with glandular hairs; stamens 4 (or 5), hypogynous, the filaments to 0.5 mm long, the anthers broadly obovoid, 1–3 times length of filaments, dehiscing slightly to conspicuously divergent upward from lateral; ovary ovoid to subglobose, puberulent with glandular hairs, the style conical to short-columnar, to 0.75 mm long, equaling to slightly exceeding ovary in length when in flower, the stigma 3- or 4-lobed. Fruits ovoid to subglobose at submaturity, 1.5–2 × 1–1.5 mm, style persistent but somewhat obscured by expanding ovary.

DISTRIBUTION. Foothills of Sierra Madre, from southeastern Jalisco through northern Colima to southwestern Michoacán, 800–1800 m alt. (see MAP 4).

HABITAT. Collected on steep hillsides above coffee plantations in association with species of *Juglans* L. and *Ficus*; in “precipitous wooded ferny barrancas”; in densely wooded arroyos with *Ficus* and various lianas; and on more open rocky slopes and ledges with *Bursera*, *Acacia* Miller, *Agave* L., woody Umbelliferae, and various orchids and bromeliads. All of these habitats feature steep terrain in an area where water is generally abundant during the rainy season but limited or absent during the dry season (mid-elevation subdeciduous forest).

PHENOLOGY. Flowering late May through June. Semimature fruits collected in mid-August.

REPRESENTATIVE SPECIMENS. **Mexico.** JALISCO: 1 km ESE of Ayotitlán (27 km por camino al E de Cuautitlán), *Cochrane et al.* 10877 (NY); 3.3 km SSE of El Chante, halfway to Tecopatlán Valley, *Iltis & Nee* 1416 (NY); 0.5–1 km NW of Rincón de Manantlán (13 km S of El Chante), *Iltis et al.* 2559 (NY). COLIMA: just S of San Antonio on road to Comala, *Bornstein & Chase* 95 (MICH); dirt road 3.5 mi N of San Antonio, *Chase* 83112 (MICH); 1–1.5 mi S of Hacienda San Antonio, SW foothills of Nevado de Colima, *McVaugh*



MAP 4. Distribution of *Piper michelianum* (stars), *P. rosei* (circles), and *P. stipula-ceum* (squares).

16107 (MICH). MICHOACÁN: San José, in distr. of Coalcomán, *Hinton 13836* (ENCB, ILL, NA, NY, US).

TAXONOMIC NOTE. *Piper michelianum* and *Piper mas* were described on the basis of the same type material and are therefore nomenclatural synonyms.

Piper michelianum is distinguished by the combination of shallowly to moderately cordate leaf blades puberulent above and puberulent to transiently pubescent beneath, glabrous to puberulent rachis and floral bracts, narrow and elongate (usually 1.5–2.5 mm long) mature pedicels, and hypogynous stamens (usually 4).

Potentially confused with *Piper rosei* where their ranges overlap, *P. michelianum* lacks the conspicuous pubescence of the rachis and bracts and has narrower and slightly longer pedicels, as well as acuminate (vs. long-acuminate), basally cordate (vs. rounded) leaves that are more conspicuously pubescent beneath.

The Iltis collections from Jalisco are sterile and are therefore included here on a tentative basis. In sterile condition *Piper michelianum* resembles *P. brachypus* and *P. mcvaughii*, both of which are also glabrous to puberulent vegetatively. The only means for separating the three species morphologically is by examining the inflorescences. I have placed these two collections under *P. michelianum* on the basis of their habitat and distribution.

9. **Piper muelleri** C. DC. in A. DC. Prodr. **16**(1): 243. 1869. TYPE: Mexico, Veracruz, Orizaba, 1853, *Mueller 180* (holotype, BR!; isotypes, G!, GH!, ILL!, LE!, NY!).

FIGURE 13.



FIGURE 13. *Piper muelleri*: A, fruiting branch, $\times 0.4$, with detailed insets of lower leaf surface showing indument, and prophyll and young inflorescence emergent from next-oldest prophyll (absent); B, portion of semimature infructescence, $\times 6$; C, portion of mature infructescence (note recurved stigmas), $\times 6$.

Habit unknown, probably small to medium-sized shrub; young branches puberulent with eglandular hairs; older branches glabrous. Prophylls 0.5–1.2 mm long, slender, base truncate, apex acute, abaxially puberulent to pubescent with eglandular hairs. Leaves with petiole 0.6–1.8 cm long, stout, puberulent to densely pubescent with eglandular hairs; blade lance-elliptic to lance-ovate

to rarely ovate, (7.3–)8.8–15.3 × 3.4–6 cm, rounded and symmetrical at base, acuminate to long-acuminate at apex, occasionally drying rugulose to bullate, 5- to 7-nerved (3 most central protracted to apex), glabrous above, densely pubescent beneath (especially along major veins) with eglandular hairs. Inflorescences 5–8.3 cm long; peduncle narrow, puberulent to pubescent, remaining rachis puberulent with eglandular hairs; bracts subsessile to minutely petiolate, 0.5–1.25 mm long, the apical region broadly spatulate-cupulate to cupulate, abaxially pubescent with eglandular hairs. Flowers with pedicel 0.5–2.5 mm long, sparsely puberulent to puberulent with eglandular hairs; stamens 5 to 7, hypogynous, the filaments to 1 mm long, equaling or slightly surpassing ovary length in flower or young fruit, the anthers subglobose, dehiscing laterally; ovary depressed-ovoid, glabrous, the style elongate, 1–1.5 times ovary length in flower, becoming largely obliterated during fruit maturation, the stigma (2- or) 3- or 4- (or 5-)lobed, with lobes recurved, persistent in fruit. Fruits depressed-ovoid when young, becoming globose at maturity, glabrous.

DISTRIBUTION. Eastern slopes of Sierra Madre Oriental, from Coscomatepec south to Orizaba in Veracruz (see MAP 3).

HABITAT. Essentially unknown, although two collections (*Matuda 1515* and *Seler & Seler 5172*) are from high elevations on mountains.

PHENOLOGY. Flowering in May, perhaps also in late April and early June. Fruits occurring from May until August or later.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Orizaba, *Botteri 192* (= 1156) (GH, K, US (2 sheets)); Cerro Punta Coscomat, *Matuda 1515* (A, MICH, MO, NY); Córdoba, Cerro de Chocamán, *Seler & Seler 5172* (GH, US).

Piper muelleri is distinguished from its closest relatives, *P. neesianum* and *P. yucatanense*, by its pubescent (vs. glabrous) plants, its comparatively long staminal filaments, and its uniquely shaped gynoecium.

Piper muelleri is perhaps the rarest species of the subgenus. It has not been collected since 1937, despite my efforts in recent years. With the continued destruction of tropical forests in many areas of Mexico, including the area surrounding Orizaba, it would not be surprising if this species were extinct. However, because I had very little information to guide me in my quest, it may simply be a matter of looking in the wrong place. I suspect that an exhaustive search of the region between Coscomatepec and Orizaba during the month of May could be rewarding and could thereby provide more detailed information concerning this species.

10. ***Piper neesianum*** C. DC. in A. DC. Prodr. 16(1): 256. 1869. TYPE: Mexico, locality unknown, 1841–42, *Karwinski 823* (holotype, LE; isotypes, G!, H!). FIGURE 14.

Arctottonia sempervirens Trel. ex Lundell, Publ. Carnegie Inst. Wash. 436: 302. 1934, *nomen nudum*. *Arctottonia sempervirens* Trel. ex Standley, Field Mus. Nat. Hist., Bot. Ser. 12: 405. 1936. *Piper sempervirens* (Trel. ex Standley) Lundell, Publ. Carnegie Inst. Wash. 478: 208. 1937. TYPE: Guatemala, Petén, Uaxactún, 16 April 1931, *Bartlett 12563* (holotype, MICH!; isotypes, ILL (2 sheets)!).

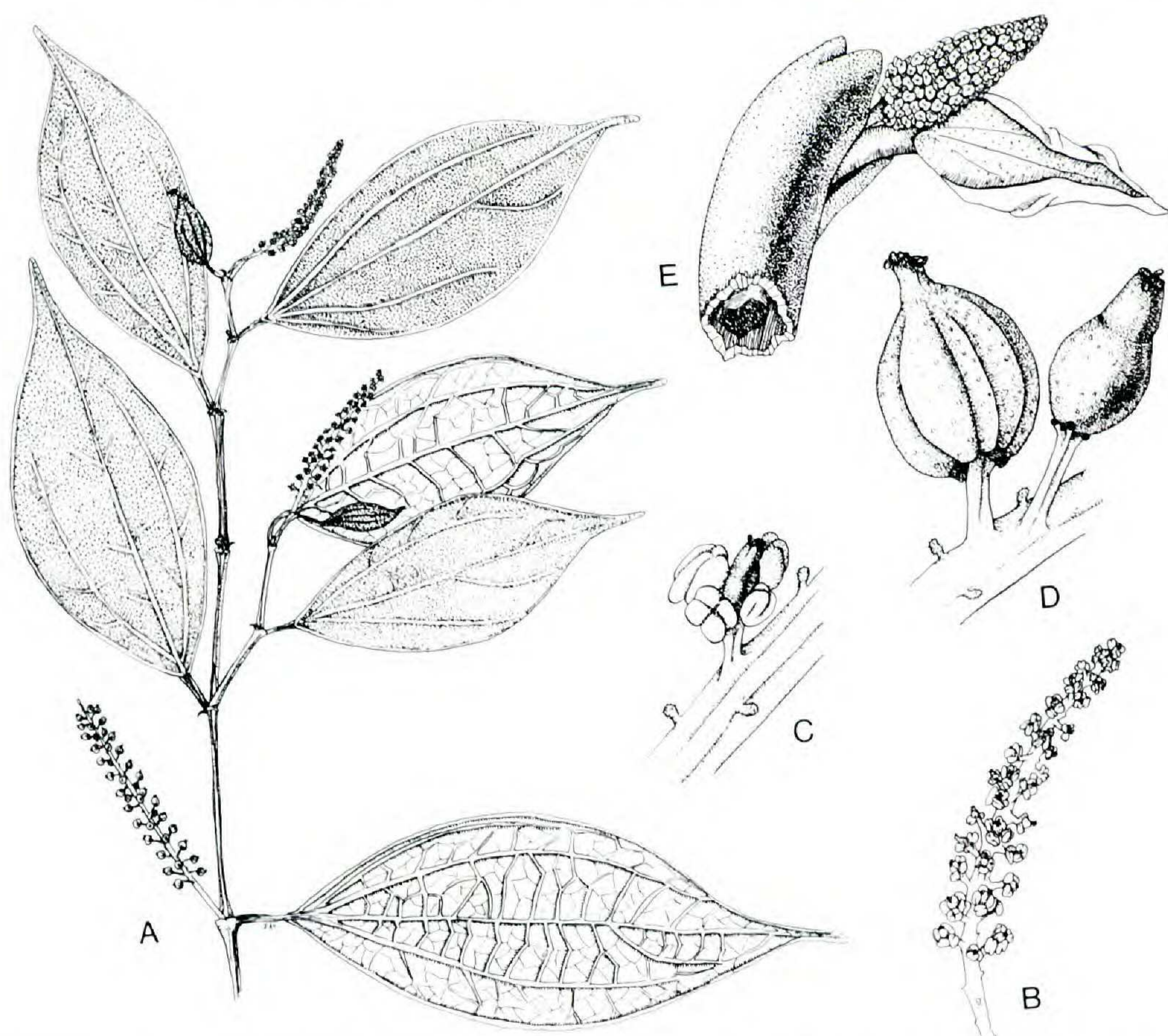


FIGURE 14. *Piper neesianum*: A, flowering branch, $\times 0.4$; B, inflorescence, $\times 1.7$; C, flower with bracts, $\times 10.5$; D, immature and mature fruits with bracts, $\times 8.4$; E, prophyll with emergent young leaf and inflorescence, $\times 8.4$.

Slender shrub, multibranched from base, 1–6.5 m tall; bark green on young branches, becoming brown and warty with age. Prophylls to 0.5 mm long, base truncate, apex acute, appearing glabrous but with glandular hairs. Leaves with petiole 2–12 mm long, stout, with glabrescent glandular hairs; blade lance-elliptic to elliptic to ovate-elliptic, 5.2–12.6(–15.2) $\times$ 1.9–6.1 cm, rounded to more commonly acute, slightly unequal and occasionally auriculate at base, abruptly acuminate to long-acuminate at apex, stiff and coriaceous, 3-nerved (central nerve protracted to apex), dark shiny green above, gray-green to silvery beneath, both surfaces appearing glabrous but with glandular hairs (at least when young). Inflorescences (2.4–)3–6.9 cm long, white at maturity; peduncle slender, rachis appearing glabrous but with glandular hairs; bracts occasionally petiolate, narrowly spatulate to spatulate to rarely spatulate-cupulate, 0.25–0.5 mm long, glabrous. Flowers with pedicel 0.5–2.5(–3.5) mm long, lax, divaricate, appearing glabrous but with very sparse glandular hairs; stamens (3 or) 4 or 5 (or 6), the filaments ca. 0.25 mm long, the anthers subglobose, dehiscing laterally or occasionally slightly upward from lateral; ovary ovoid to rarely ellipsoid, puberulent with glandular hairs, the style conical, $\frac{1}{4}$ to equal ovary in length, indistinct when young, becoming more distinct with age, the stigma (2- or) 3- to 5- (or 6-)lobed, persistent in fruit. Fruits ovoid-ellipsoid to globose,

2–2.5 × 1.5–2 mm, conspicuously ribbed on drying, with sparse glandular hairs.

DISTRIBUTION. Largely restricted to Yucatán Peninsula, especially central and southern portions; also extending into Chiapas and Veracruz (see MAP 3).

HABITAT. Originally occurring in “ramonales,” upland climax subdeciduous forests developing on calcareous soils and dominated by the breadnut tree, *Brosimum alicastrum* (Moraceae). This vegetation type was typical of the Yucatán Peninsula until 20–25 years ago, when agricultural demands resulted in destruction of large areas of natural vegetation. Currently, therefore, *Piper neesianum* is usually found at the edge of disturbed secondary forests, at 20–400(–700) m alt., where it is one of the more common understory shrubs. In more remote areas of the Yucatán Peninsula, such as portions of the Petén region of Guatemala, one should still be able to find this species in its undisturbed native habitat.

PHENOLOGY. Flowering February to June, but most prominently in April and May; specimens with mature fruits collected from June to November.

REPRESENTATIVE SPECIMENS. **Mexico.** VERACRUZ: Papantla, *Liebmann 18* (G, K, US); Lomas al sur del Poblado 11, ca. 30 km E del campamento La Laguna, Minantitlán, *Wendt et al. 2633* (ENCB, MEXU, NY). CHIAPAS: 20 mi N of Ocozocoautla, near km 31 marker, toward Apitpac, *Croat 40640* (MO); camino a Jato del Tigre, cerca Laguna Galón, *Miranda 6245* (MEXU); near El Ocote, 30 km NW of Ocozocoautla, *Miranda 6252* (MEXU, US). TABASCO: 100 m del limite con México sobre carretera 15-E, *Novelo et al. 178* (MEXU). CAMPECHE: along Hwy. 186 between Escárcega and Xpujil at km 87 marker, *Bornstein & Chase 69* (MICH); Campo Experimental Forestal Tropical “El Tormento,” km 5 on road between Escárcega & Candelaria, *Chavelas ES-932* (MEXU), *ES-1041* (MEXU), *ES-1553* (MEXU), *ES-1631* (MEXU); zona arqueológica de Becan, Loma central, *Cowan 2997* (ENCB, MEXU); Tecolutla, *Liebmann 17* (G, GH); Reforma, *Lundell 834* (F, ILL, MICH, MO, US); Pixoyal, *Ross 128* (GH, MEXU, US); 14 km S of Xpujil, *Shepherd 68* (ENCB, MICH). YUCATÁN: Chichén Itzá, *Lundell 7406* (F, GH, MICH (2 sheets), NY, TEX, US). QUINTANA ROO: along Bacalar shoreline pkwy., 1.1 km S of school, *Bornstein & Rutledge 27* (MICH); 1.9 km S of Bacalar–Cenote Azul turnoff along Hwy. 307, *Bornstein & Rutledge 30* (MICH); 0.3 km SE of km 20 marker along Hwy. 196, *Bornstein & Rutledge 33* (MICH); along Hwy. 186 between Escárcega and Chetumal, 1.9 km E of km 225 marker, *Bornstein & Rutledge 38* (MICH); Lake Chichankanab, *Gaumer 23678* (F, GH, MO, NY, US); 26 km S of Tulum, *Téllez & Cabrera 2606* (MEXU); 8 km NE of Felipe Carillo Puerto, sobre camino a Vigio Chico, *Téllez & Cabrera 2838* (MEXU). **Belize.** BELIZE: Gracie Rock, 1.5 mi S of mi 22 on Western Hwy., *Dwyer 10940* (K, MO, NA, WIS). CAYO: 9.5 mi S of Georgeville on road to Augustine, *Croat 23440* (ENCB, F, GH, MEXU, MO, TEX); Chalillo Crossing, *Lundell 6510* (F, GH, MICH, NY, TEX, US). **Guatemala.** PETÉN: Uaxactún, *Bartlett 12326* (ILL, MICH, NY, UC, US); 10 km E of Remate, *Contreras 916* (F, G, MEXU, TEX, US); 22 km W of Remate, *Contreras 1033* (MICH, TEX (2 sheets), US); Tikal Natl. Park, *Contreras 1246* (G, MICH, TEX, US); Lake Macanche, *Contreras 5518* (F, MO, NY, US); Lake Petén Itzá, Santa Elena, *Contreras 5763* (F, GH, TEX); Macanche, *Contreras 5840* (F, GH, TEX, US); km 32 bordering Melchor de Mencos road, *Contreras 5863* (GH, TEX); N shore of Lake Yaxhá, *Croat 24680* (BR, MO); Carmelita, *Egler 42-234* (F, TEX); El Paso, *Lundell 1457* (GH, MICH, NY, US); La Libertad, *Lundell 3500* (F, ILL, MICH, US); Ixlu, *Lundell 3828* (ILL, MICH, TEX); 35 km E of Santa Elena, *Molina 15482* (F, NY); Santa Elena, km 6 on road to San Andres, *Ortíz 1978* (F, MO, NY, US); 2 km NE of Uaxactún, *Ortíz 2609* (F, MICH, US); bordering Lake Macanche, 35 km from Flores, *Ortíz 2696* (F, MICH, US); Cerro

Ceibal, between mouth of Río Santa Monica & Río San Martín, *Steysmark 46061* (F, MICH (2 sheets), NY, US). ALTA VERAPAZ: Cerro Chinaja between Finca Yalpemech and Chinaja, *Steysmark 45581* (F, MICH). IZABAL: Cienaga, on Petén–Guatemala road, *Contreras 10851* (MEXU, MO, TEX, US).

Piper neesianum is commonly confused with its sympatric congener, *P. yucatanense*. Both species have leaves distinctly longer than broad, but *P. neesianum* has a more dense, shrubby habit; firm, shiny, nonrugulose (vs. membranous, dull, and rugulose or bullate) leaves; smaller, narrower floral bracts; and conspicuously ribbed (vs. smooth) fruits (especially when dry). A third species with lance-ovate leaves, *P. muelleri*, has rarely also been mistaken for *P. neesianum*. However, it can be easily distinguished by its rather heavy indument of eglandular hairs along the veins on the leaf undersurface, its pubescent floral bracts and rachis, its long staminal filaments, and its uniquely shaped gynoecium.

11. *Piper novogalicianum* Bornstein, sp. nov.

FIGURE 15.

Frutex 1.5–5 m altus, ramunculis puberulis ad dense pubescentibus; prophyllum usque ad 1 cm longum, puberulum vel dense pubescens; folia laminis ovatis vel late ovatis vel suborbiculatis, 4.9–13.2 × 4.1–11.5(–13.5) cm, breviusculis vel acuminatis, basi rotundatis vel cordatis, supra puberulis vel pubescentibus, subter puberulis vel pubescentibus vel tomentosis; inflorescentia 6.2–14.3(–16) cm longa, rachidi sparsim ad dense pubescenti; bracteae usque ad 0.75 mm longae, spatulatae vel spatulicupulatae, sparsim puberulae vel pubescentes vel dense pubescentes; pedicelli 0.5–1.5(–2) mm longi; stamina hypogyna vel interdum ut videtur basi ovarii adnata; ovarium ellipsoideum vel subglobosum; stylus depresso-ovoideus vel breviconicus vel brevicolumnaris, 0.5–0.75 mm longus; fructus immaturus transverse-ellipsoideus, puberulus.

TYPE. Mexico, Jalisco, 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, 300 m alt., 20 June 1983, *Bornstein 99* (holotype, MICH; isotypes, CHAP, GH, INIF, MEXU, NY).

Small to medium-sized shrub, often treelike, 1.5–5 m tall; youngest twigs puberulent to densely pubescent, glabrescent, the hairs predominantly eglandular; older stems gray-brown to ash-gray, with swollen nodes and round, warty lenticels, maximum diameter to 6 cm. Prophylls to 1 cm long, base truncate, apex acute, abaxially puberulent to densely pubescent with eglandular hairs. Leaves with petiole 0.4–2.7 cm long, narrow to moderately broad, pubescent to densely long-pubescent with eglandular hairs; blade ovate to broadly ovate to suborbiculate, 4.9–13.2 × 4.1–11.5(–13.5) cm, truncate to rounded to cordate at base, gradually short-acuminate to acuminate at apex, 5- to 7- (to 9-)nerved, puberulent to pubescent above with both hair types in ± equal abundance, puberulent to pubescent to tomentose beneath with eglandular hairs predominant along and ± restricted to major veins. Inflorescences 6.2–14.3(–16) cm long, yellowish white to white; peduncle puberulent to pubescent with eglandular hairs, remaining rachis sparsely pubescent to pubescent with eglan-

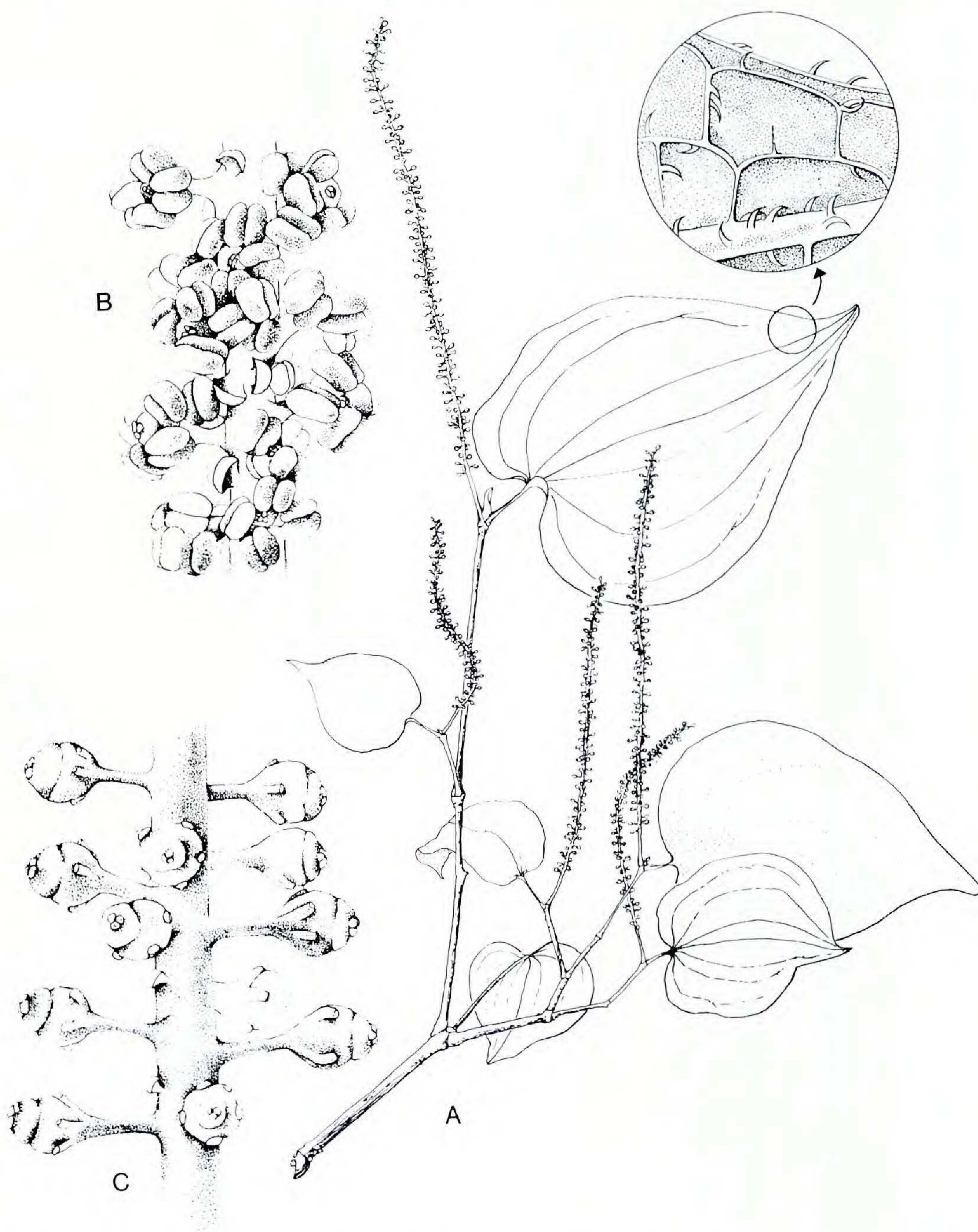


FIGURE 15. *Piper novogalicianum*: A, flowering branch, $\times 0.42$, with detailed inset of lower leaf surface to show indument; B, portion of inflorescence, $\times 6.3$; C, portion of infructescence, $\times 6.3$.

dular hairs; bracts sessile to subsessile, spatulate to spatulate-cupulate, to 0.75 mm long, abaxially sparsely puberulent to densely pubescent with eglandular hairs. Flowers with pedicel (0.5–)1–1.5(–2) mm long, usually puberulent with glandular and/or eglandular hairs; stamens 4 to 6 (or 7), hypogynous or occasionally appearing as if adnate to base of ovary, filaments and anthers $\pm$ equal in length (to 0.5 mm), anthers dehiscing slightly to conspicuously upward from lateral; ovary ellipsoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to short-conical or short-columnar, 0.5–0.75 mm

long, ca. $\frac{1}{2}$ to equal length of ovary when in flower, the stigma 3- to 5-lobed. Fruits (when partially mature) transversely ellipsoid, ca. 1×1.5 mm, puberulent, style persistent.

DISTRIBUTION. Southwestern Jalisco and neighboring Colima; disjunct in state of Mexico (see MAP 2).

HABITAT. Steep hillsides in subdeciduous forests, from near sea level to 1350 m alt.; apparently also in second-growth woodlots, especially inland and at higher elevations.

PHENOLOGY. Flowering May to mid-July or into August. Fruits appearing as early as mid-June, but most commonly July to September.

SPECIMENS EXAMINED. **Mexico.** JALISCO: 1 km NE of Cihuatlán along small stream parallel to Río Cihuatlán, *Bornstein & Hensold* 5 (MICH); 2 km S of La Manzanilla on road to Tamarindo beach, *Bornstein & Hensold* 8 (MICH); along Hwy. 80 between Autlán and Melaque, 4 km N of side road to Casimir Castillo, *Bornstein* 76 (MICH); ca. 11 km S of Autlán on Hwy. 80 to Barra de Navidad, *Bornstein* 96 (MICH); Santa Cruz, *Delgado* 348 & *Hernández* 2599 (ENCB, MEXU); ca. 22 mi SSW of Autlán, *Wilbur* 1589 (MICH); 0.5 mi N of La Resolana, *Wilbur* 1591 (MICH); 2 mi W of Autlán, *Wilbur* 1675 (MICH). COLIMA: 2.5 km S of coastal Hwy. 200, W of Santiago along gravelly dirt road to Vida del Mar, *Bornstein & Hensold* 2 (MICH); 5 mi W of Santiago, then 2.5 mi on road to Peña Blanca, *McVaugh* 15691 (MICH). MEXICO: Tejupilco in district of Temascaltepec, *Hinton* 4287 (ILL, K, MICH, NA, US).

In my dissertation (Bornstein, 1985) I recognized the high-elevation collections (*Bornstein* 96, *Hinton* 4287, *Wilbur* 1675) as a distinct species, *Piper tejupicoanum* Trel. ex Bornstein, with the Hinton collection at MICH designated as the holotype. At that time I also noted my concern about the recognition of this taxon, since the characters that serve as the basis for the distinction (i.e., leaf size and pubescence, rachis and bract pubescence, and pedicel length) are usually rather variable. After reconsidering this situation, I have decided to recognize a single variable species, *P. novogalicianum*, while noting that the populations at high elevations apparently represent one extreme in which the leaves are smaller and the plant parts more pubescent. This matter will only be settled with additional collecting (especially of flowers and fruits from the same plant), as well as field studies of populations at various elevations.

This species, as presently circumscribed, is distinguished from *Piper brevipedicellatum* on the basis of having longer and narrower pedicels.

12. ***Piper rosei*** C. DC. *Annuaire Conserv. Jard. Bot. Genève* **21**: 316. 1920.
TYPE: Mexico, Sinaloa, Colomas, 13–20 July 1897, *Rose* 3234 (lectotype, here chosen, US 302199!). FIGURE 16.

Piper rosei C. DC. ex Trel. *Amer. J. Bot.* **8**: 215. 1921. TYPE: Mexico, Sinaloa, Colomas, 13–20 July 1897, *Rose* 3234 (holotype, US!).

Piper diguetianum Trel. *Amer. J. Bot.* **8**: 215. 1921. TYPE: Mexico, Jalisco, *Diguet* s.n. (holotype, US!).

Medium-sized treelike shrub, 2–5 m tall; youngest twigs glabrous to puberulent with short eglandular hairs; older branches soon glabrous, with brown,

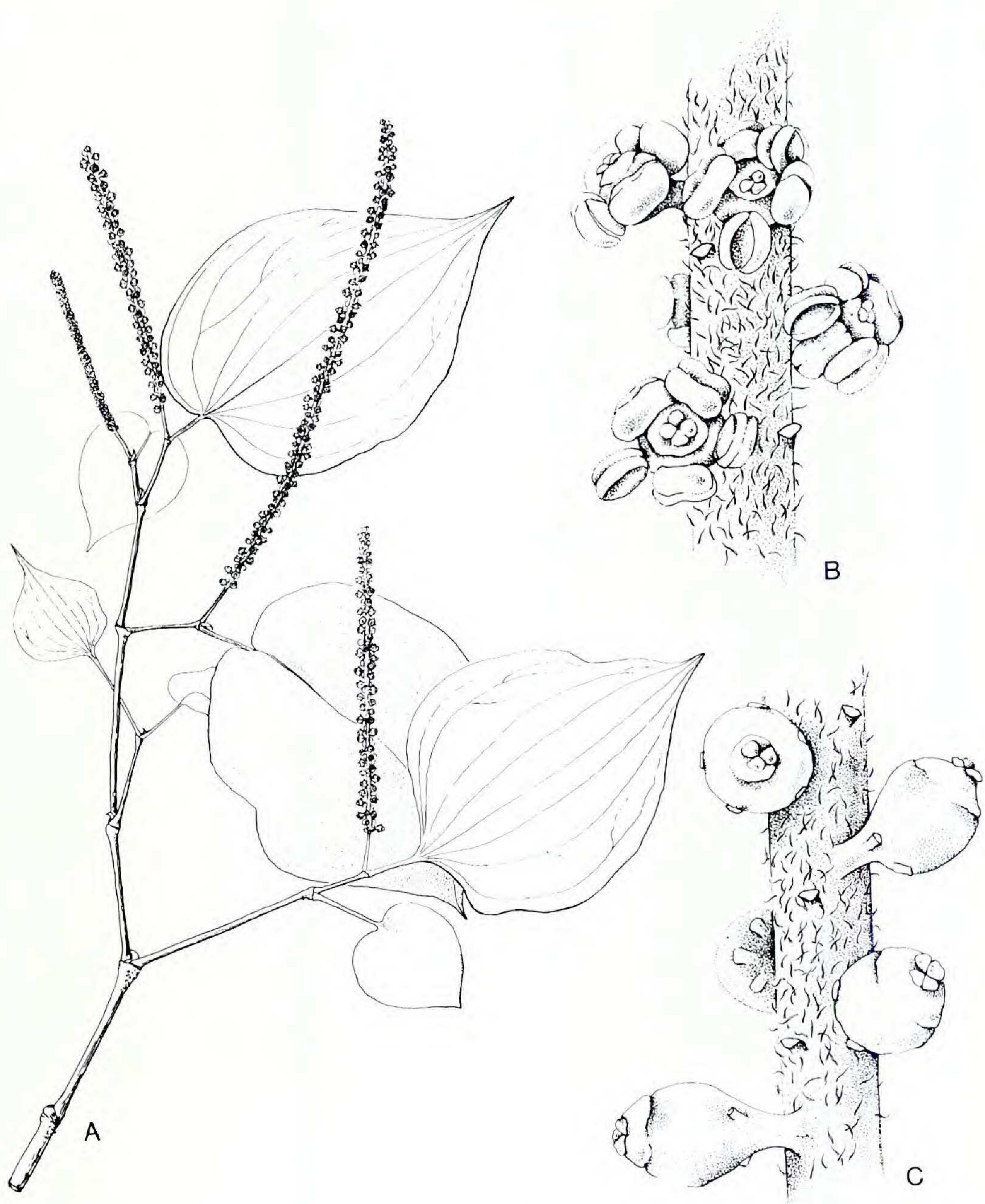


FIGURE 16. *Piper rosei*: A, flowering and fruiting branch, $\times 0.42$; B, portion of inflorescence, $\times 6.3$; C, portion of infructescence, $\times 6.3$.

elliptic, warty lenticels, maximum diameter to 7.5 cm. Prophylls to 10 mm long, base truncate, apex acute, glabrous to puberulent with short eglandular hairs. Leaves with petiole 0.7–1.9(–3.1) cm long, narrow, glabrous to puberulent with glandular and eglandular hairs; blade ovate to most commonly broadly ovate to suborbiculate, (5.3–)6.7–13(–15.6) $\times$ 4.2–12.1 cm, rounded to shallowly cordate at base, short- to long-acuminate at apex, 5- (to 7-)nerved, glabrous to puberulent, the hairs largely restricted to petiole-blade junction, glandular and short eglandular. Inflorescences (5–)6.3–15.5 cm long, greenish yellow when young, white to cream colored in full flower; peduncle glabrous to sparsely pubescent, remaining rachis sparsely to densely pubescent with eglandular hairs;

bracts sessile to subsessile, spatulate to cupulate, 0.25–0.75 mm long, sparsely pubescent to pubescent (often on both surfaces, but especially abaxially and marginally) with eglandular hairs. Flowers with pedicel 0.5–1.5(–1.75) mm long, usually glabrous to puberulent, but occasionally sparsely pubescent near base with both glandular and eglandular hairs; stamens (3 or) 4 or 5 (or 6), hypogynous but often appearing adnate to base of ovary, filaments and anthers to 0.5 mm long, anthers dehiscing laterally or conspicuously upward from lateral; ovary ovoid-ellipsoid to widely depressed-ovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to short-conical to short-columnar, from $\frac{1}{4}$ to equal length of ovary when in flower, the stigma 3- to 5-lobed. Fruits subglobose to globose, 1–2 × 1–2 mm, puberulent, style becoming obscure with fruit maturation.

DISTRIBUTION. Southern Sinaloa south through southwestern Jalisco and northern Colima (see MAP 4). Apparently absent from Nayarit (probably a reflection of limited collecting throughout Nueva Galicia).

HABITAT. Prefers steep hillsides or slopes in relatively open, disturbed, semi-deciduous or deciduous forests. At low elevations found with other pipers in the coastal palm forests dominated by *Orbignya cohune*. At high elevations occurring in oak forests, above coffee plantations, and in forests dominated by *Bursera* spp. From near sea level to 1400 m, but mostly below 1000 m alt.

PHENOLOGY. Flowering late May to early July. Young fruits appear by mid-June; mature fruits collected in September and October. A second period of flowering may also occur at this time (end of rainy season).

REPRESENTATIVE SPECIMENS. **Mexico.** SINALOA: Colomas, *Rose 1657* (GH, K, US); Copalita, *Moran 13310* (UC). JALISCO: ca. 2 km S of La Manzanilla on road to Tamarindo beach, *Bornstein & Hensold 6* (MICH); ca. 15 km S of Autlán on Hwy. 80 toward Barra de Navidad, *Bornstein 97* (MICH); 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, *Bornstein 100* (MICH); 4 mi NE of Talpa, *Chase 83127* (MICH); 5 mi S of Talpa on road to Tomatlán, *Chase 83129* (MICH); 16 km N of Mascota on road between Mascota and San Sebastián, *Lott et al. 1349* (MICH); ca. 5.5 mi N of Tecalitlán, *McVaugh 15436* (MICH); ca. 16.9 mi NW of Hwy. 80–200 junction (near Melaque) along Hwy. 200, *Stevens & Fairhurst 1868* (ENCB, TEX); 8 mi S of Autlán toward La Resolana, *Wilbur 2190* (MICH). COLIMA: 1.3 mi W of San Antonio, *Chase 83113* (MICH).

TAXONOMIC NOTES. *Piper rosei* C. DC. and *P. rosei* C. DC. ex Trel. are independent descriptions based on the same type material; i.e., they are nomenclatural synonyms. De Candolle examined the Rose collections at us in the late 1890's, apparently supplying a name for the collections but not publishing it until over 20 years later. Trelease saw these same Rose collections while preparing his first publication on the Piperaceae and adopted the herbarium epithet suggested by De Candolle. De Candolle's treatment of the Mexican Piperaceae was published several months prior to Trelease's treatment of the North American pipers of sect. *Ottonia*, and therefore Trelease's name is an illegitimate later homonym.

The characters cited by Trelease to distinguish *Piper diguetianum* and *P. rosei* are not reliable. The racemes in the former are shorter because they are

obviously broken. The pedicel length difference (1.5 vs. 1 mm, respectively) is a result of the level of floral maturation: the flowers of the Rose collections are considerably younger, and therefore the pedicel has not fully elongated. The third distinction, stamen number (5 vs. 3 or 4), has been shown to be a poor character on which to base species differences. Again examining the Rose material, I have seen numerous flowers with five stamens in addition to those with three or four.

In my original investigation of this species (Bornstein, 1985), I separated the low-elevation collections (*Stevens & Fairhurst 1868*; *Bornstein & Hensold 6, 7, & 9*) as a distinct taxon, *Piper palmicola* Bornstein, with the Stevens & Fairhurst collection at TEX designated as the holotype. This species was recognized as distinct on the basis of its less-pubescent floral rachis and bracts, its short-acuminate to acuminate leaf apex, and its shorter (0.5–1 vs. 1–1.5 mm) pedicels. After further consideration, I have decided that these features either are essentially continuous (pedicel length) or are too variable (pubescence and leaf shape) to warrant the recognition of *P. palmicola*, which remains an unpublished name, and I have consequently interpreted *P. rosei* in a rather broad sense. The low-elevation collections form a group that tends to obscure the boundary between *P. brachypus* and *P. rosei*, strongly suggesting that these two species are closely related.

13. **Piper stipulaceum** Opiz in Presl, Reliq. Haenk. 1(3): 160. 1828. TYPE: Mexico, locality unknown, *Haenke s.n.* (lectotype, here chosen, PR!; isolectotypes, B (destroyed?), PR!). FIGURE 17.

Enckea stipulacea (Opiz) Kunth, Linnaea 13: 600. 1838. *Ottonia stipulacea* (Opiz) Presl, Epimel. Bot. 231. 1851. *Arctotonia stipulacea* (Opiz) Trel. Proc. Amer. Philos. Soc. 75: 716. 1935.

Piper aguilanum C. DC. Annuaire Conserv. Jard. Bot. Genève 21: 318. 1920. TYPE: Mexico, Guerrero, Santa Rosa près d'Aguila, 650 m alt., 16 July 1898, *Langlassé 248* (holotype, G!; isotypes, GH! K!, US!).

Piper albicaule Trel. Amer. J. Bot. 8: 216. pl. 8, fig. 2. 1921. TYPE: Mexico, Guerrero, Santa Rosa près d'Aguila, 650 m alt., 16 July 1898, *Langlassé 248* (holotype, US!; isotypes, G!, GH!, K!).

Medium-sized treelike shrub, sparsely branched from base, 2–4 m tall; youngest twigs pubescent to densely pubescent, glabrescent, ash-gray and with conspicuous warty brown lenticels, to ca. 5 cm in diameter. Prophylls 6–10(–15) mm long, base truncate, apex acute, abaxially pubescent to densely pubescent to occasionally tomentose with eglandular hairs. Leaves with petiole 0.6–3.5 cm long, stout, pubescent to densely soft-pubescent with eglandular hairs; blade ovate to broadly ovate-suborbiculate, (4.5–)6.3–13.7(–14.6) × (2.4–)4.8–12.6 (–14) cm, rounded to truncate to mostly shallowly cordate at base, short-acuminate to acuminate at apex, (5- to) 7- (to 9-)nerved, puberulent to pubescent above, puberulent to densely pubescent beneath especially along major veins (both hair types present, with glandular ones more prevalent in areolar regions and eglandular ones ± restricted to veins). Inflorescences (5.8–)7–12.9 cm long, yellow-green when young, whitish in full flower; peduncle stout,

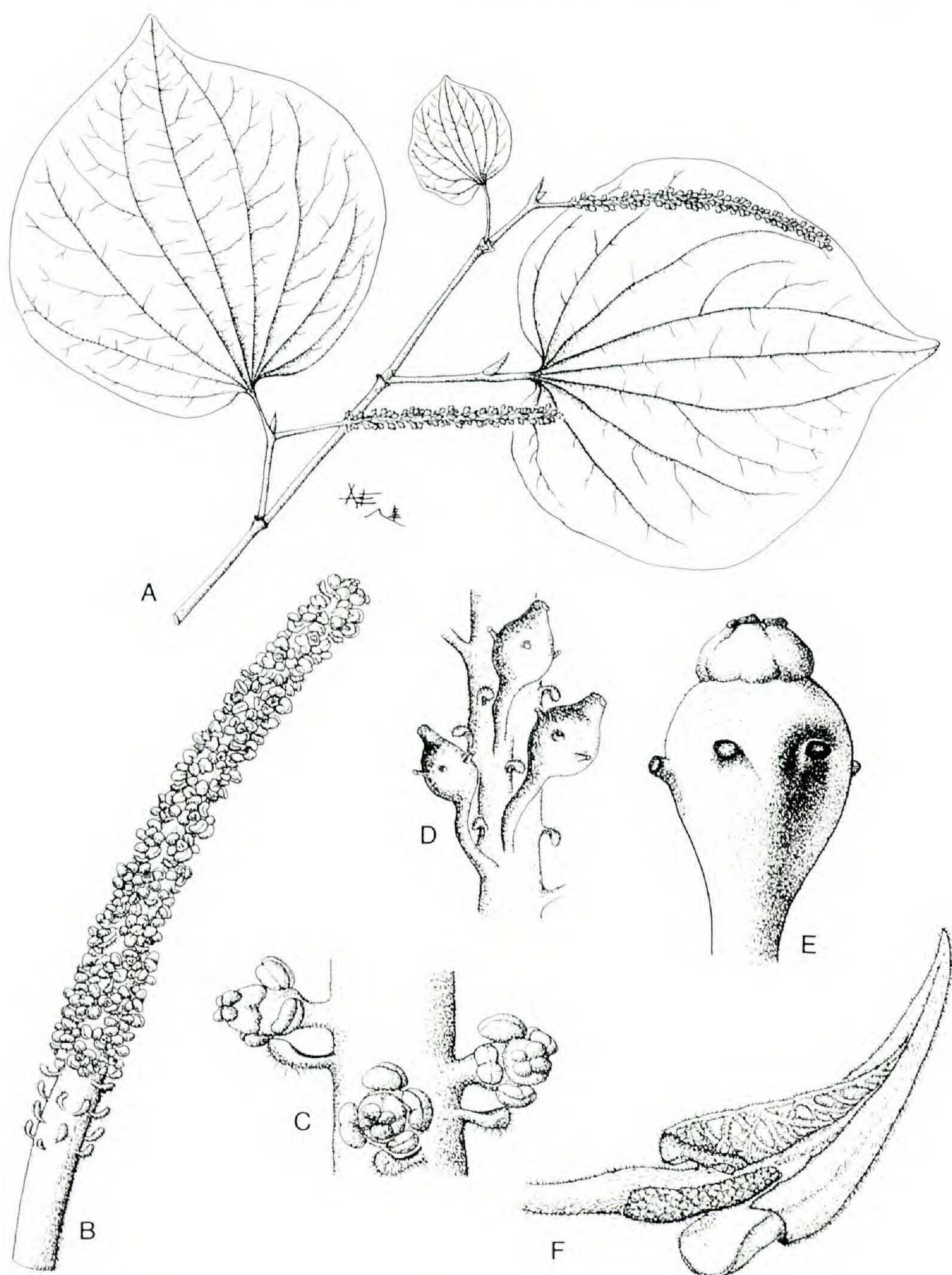


FIGURE 17. *Piper stipulaceum*: A, fruiting branch, $\times 0.43$; B, inflorescence, $\times 8.6$; C, flowers and associated bracts, $\times 8.6$; D, portion of young infructescence, $\times 8.6$; E, mature fruit, $\times 12.9$; F, prophyll with emergent young leaf and inflorescence, $\times 8.6$.

puberulent to pubescent at base with glandular and eglandular hairs, gradually transitional to glabrous to puberulent to sparsely pubescent rachis; bracts occasionally sessile, but usually with narrow stalklike basal portion that broadens gradually to abruptly into narrow to broadly spatulate to spatulate-cupulate apical region, 0.5–0.75(–1.25) mm long, abaxially puberulent to pubescent. Flowers with pedicel 0.5–2 mm long, ca. 0.5 mm wide, glabrous to puberulent with glandular hairs; stamens 4 or 5 (or 6), adnate to ovary from near base to

middle, the filaments to ca. 0.5 mm long, the anthers depressed-ovoid, usually longer than filaments, dehiscing laterally or occasionally slightly divergent upward; ovary ovoid to subglobose, puberulent with glandular hairs, the style depressed-ovoid to conical, to 0.5 mm long, from $\frac{1}{3}$ to nearly equal length of ovary when in flower, the stigma 3- or 4- (or 5-)lobed. Fruits ovoid to globose to slightly obloid, usually ca. 2×2 mm, drying brown to black, with glandular hairs, the style usually persistent to some degree, but not more than $\frac{1}{3}$ length of ovary.

DISTRIBUTION. Southwestern Jalisco south to northwestern Guerrero, near Zihuatanejo, in narrow band from Pacific Ocean to foothills of Sierra Madre (see MAP 4).

HABITAT. Variable: at low elevations near coast, a relatively frequent understory shrub in palm forests dominated by *Orbignya cohune*; at higher elevations farther inland, found along edges of ravines above intermittent mountain streams in subdeciduous forests usually dominated by *Brosimum alicastrum*, *Ficus* spp., or *Bursera* spp. From near sea level to 650 m alt.

PHENOLOGY. Flowering May to July, rarely later. Young fruits appearing late May or early June; mature fruits collected from August to September, but probably persisting on plants into dry season.

SPECIMENS EXAMINED. **Mexico.** JALISCO: 5.1 km W of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, N side of road, *Bornstein* 79 (MICH); 7.9 km WNW of Hwy. 80 along Hwy. 200 toward Puerto Vallarta, S side of road, *Bornstein & Weber-Bornstein* 83 (MICH); ca. 12 km NE of Nacastillo on road to San Miguel Purificación and Purificación, *Iltis & Nee* 1531a (NY); 1–4 km E of Casimir Castillo, ca. 20 km SSW of Autlán, “Arroyo de Tacubaya,” at base of “Cerro la Petaca,” *Iltis et al.* 296 (NY); ca. 2 km N of division line of UNAM, road to Nacastillo, *Magallanes* 754 (TEX). COLIMA: 7.8 km N on Hwy. 98 toward Minatitlán, E side of road, *Bornstein* 86 (MICH); 0.5 km S of Comatlán on Hwy. 98 toward Minatitlán, E side of road, *Bornstein* 98 (MICH); Playa de Santiago, on road to Manzanillo airport, *McVaugh* 15594 (MICH). MICHOACÁN: 2 mi N of San Juan de Lima (on road to Coahuayana), *Hansen, Hansen, & Nee* 1442 (MEXU, MICH, US, WIS); La Placita (Río de Aquila), *Turner* 2035 (MICH); 1 mi E of La Placita, *Turner* 2071 (MICH). GUERRERO: Vallecitos, Montes de Oca, *Hinton* 11372 (F, K, MEXU, MO, NY, US); 2 mi E of Vallecitos de Zaragoza (between kms 52 & 53) on Hwy. 200 toward Ciudad Altamirano, *Murray & Johnson* 1433 (MICH).

TAXONOMIC NOTE. As in the *Piper michelianum*–*Piper mas* and *Piper rosei* situations, both Casimir de Candolle and William Trelease published new species, *Piper aguilanum* and *Piper albicaule*, respectively, on the basis of the same type material. These taxa are thus nomenclatural synonyms.

Piper stipulaceum is most often confused with *Piper abalienatum* because in both the stamens are adnate to the ovary (only *P. mcvaughii* also shares this character, and it is easily distinguished by its puberulent vegetative parts, very-short-pedicellate flowers, and smaller leaves). The characters and character states that I use to distinguish these two species are summarized in the TABLE. When the opposite extremes of these characters are expressed, which is frequently the case, these species are quite different and readily separable. There are, however, a few specimens that approach the established limits of the range

of the character states, often appearing to bridge the gap that separates the species. Usually all or most of these characters are affected simultaneously in a given specimen, possibly suggesting that introgressive hybridization might be the cause rather than abnormal extremes of variation. Although I have not observed these species growing together, their geographic ranges do overlap in portions of Jalisco, Colima, and Michoacán. In addition, habitat preferences of the species are similar, although *P. stipulaceum* does seem to be more restricted to cool, moist sites. Therefore, the potential for hybridization exists, as do the newly disturbed, unstable habitats that hybrids may need to become established. However, detecting and documenting introgressive hybridization would require more extensive collection of specimens in the areas of geographic overlap. In the meantime, I have placed those “intermediate” specimens in one or the other species on the basis of overall similarity using the criteria available.

A somewhat different problem occurs in trying to distinguish *Piper stipulaceum* and *P. novogalicianum*. As presently circumscribed, the taxa differ significantly only in the position of the stamens relative to the ovary (adnate and hypogynous, respectively). As I have mentioned previously for several taxa, *P. novogalicianum* among them, there is a strong tendency for the stamens to appear to be adnate to the base of the ovary. This feature is most apparent in the fruiting condition, where the ovary has expanded, thereby partially incorporating the upper portion of the pedicel (the receptacle). This, in turn, causes the stamens seemingly to “shift” to the adnate position. Since the remaining features of these two species are quite similar, this apparent change can lead to identification problems, especially with pressed specimens. To enable distinction between the taxa, flowering material should be obtained, preferably in pickled form. Fortunately, most of the specimens that I have examined have had some flowers, so that when they are restored to their original state with a detergent solution, it is possible to assign them to the appropriate species.

14. ***Piper yucatanense*** C. DC. *Linnaea* **37**: 334. 1872. TYPE: Mexico, Yucatán, July 1840, *Linden s.n.* (holotype, G!). FIGURE 18.

Piper thiemeanum Trel. *Amer. J. Bot.* **8**: 214. *pl. 5, fig. 2.* 1921. *Ottonia thiemeanum* (Trel.) Yuncker, *Ann. Missouri Bot. Gard.* **37**: 71. 1950. TYPE: Honduras, Cortés, San Pedro Sula, June 1887, *Thieme 5455* (holotype, US!; isotypes, GH!, K!, UC!, US (3 sheets)!).

Piper tatei Trel. *Amer. J. Bot.* **8**: 215. 1921. TYPE: Nicaragua, 1867–8, *Tate 367* (holotype, K!).

Piper chichankanabanum Trel. *J. Wash. Acad. Sci.* **19**: 330. 1929. TYPE: Mexico, Quintana Roo, Lake Chichankanab, April 1917, *Gaumer 23699* (holotype, F!).

Arctotonia pittieri Trel. *Proc. Amer. Philos. Soc.* **73**: 328. 1934. TYPE: Panama, Canal Zone, Alhajuela, 11–14 May 1911, *Pittier 3458* (lectotype, here chosen, F!; isolecotypes, F!, US!).

Arctotonia tuxpenyana Trel. ex Lundell, *Publ. Carnegie Inst. Wash.* **436**: 311. 1934, *nomen nudum*. *Arctotonia tuxpenyana* Trel. ex Standley, *Field Mus. Nat. Hist., Bot. Ser.* **12**: 406. 1936. *Piper tuxpenyanum* (Trel. ex Standley) Lundell, *Publ. Car-*

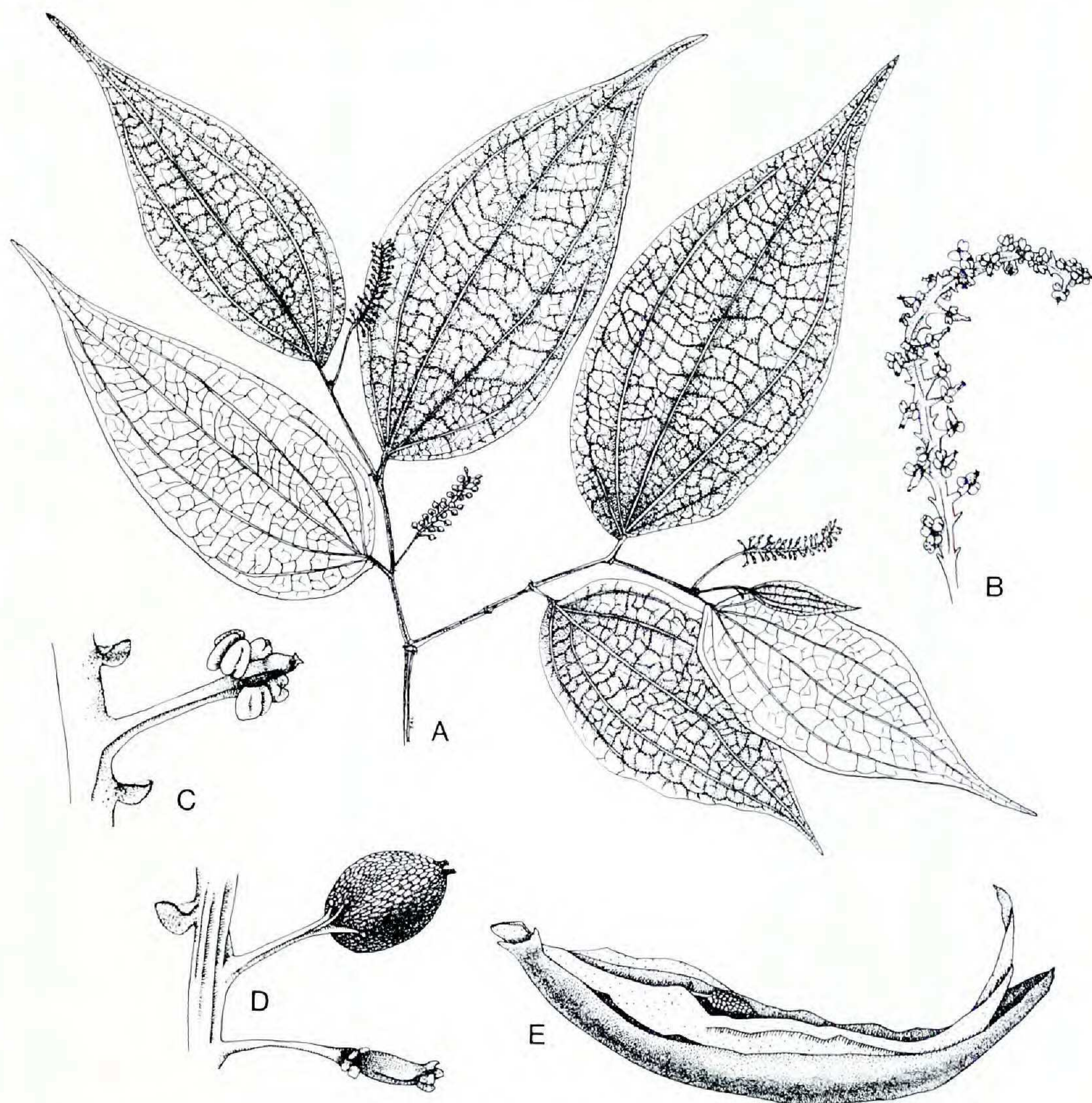
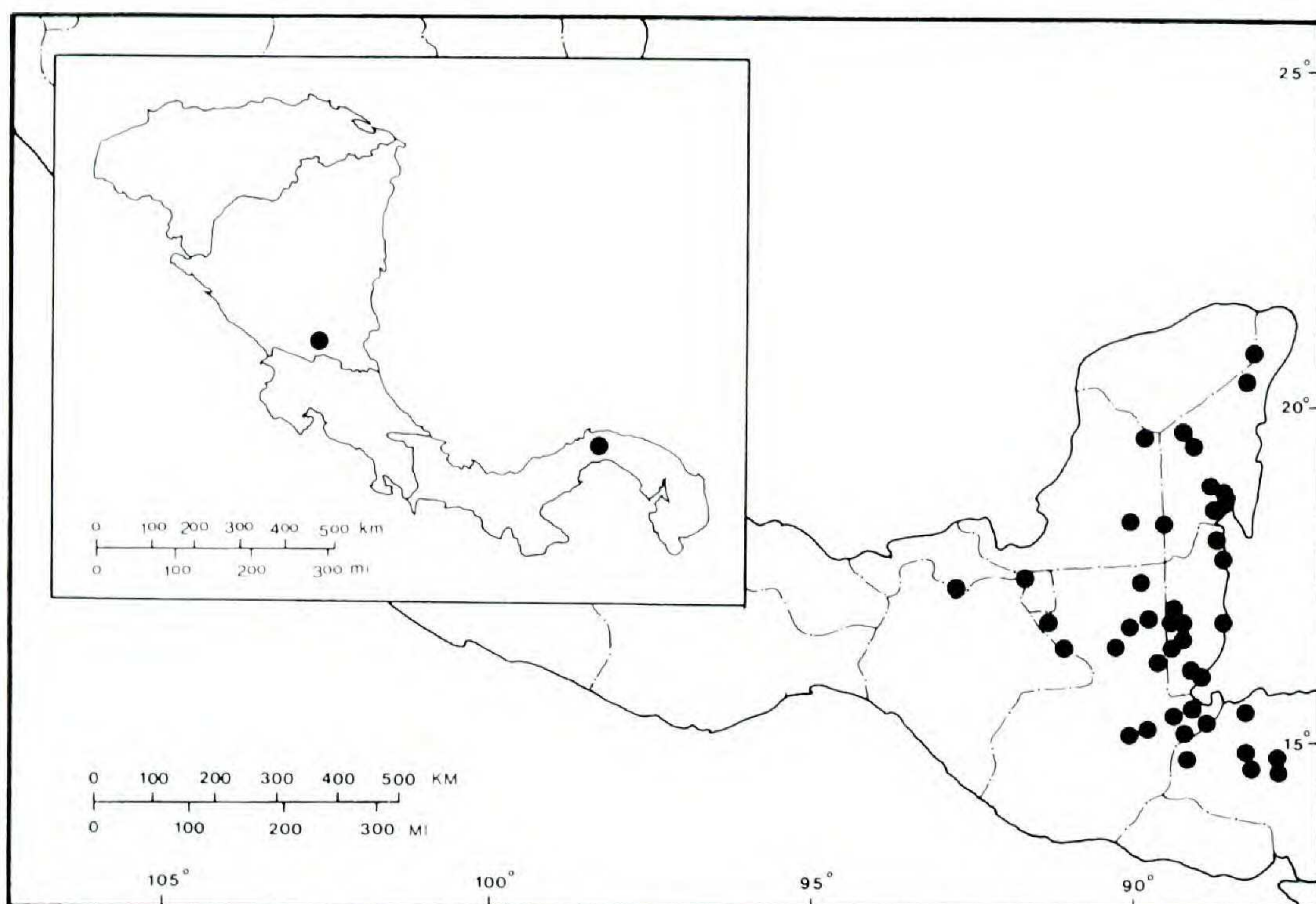


FIGURE 18. *Piper yucatanense*: A, flowering branch, $\times 0.4$; B, inflorescence, $\times 8$; C, flower with bracts, $\times 10$; D, immature (unfertilized?) and mature fruits with bract, $\times 10$; E, prophyll with emergent young leaf and inflorescence (detached and displaced from normal position), $\times 8$.

negie Inst. Wash. **478**: 208. 1937. TYPE: Mexico, Campeche, Tuxpeña, 7 Feb. 1932, *Lundell 1300* (holotype, MICH!; isotypes, F!, ILL!, NY!).

Slender, loosely branched shrub 0.5–3 m tall, appearing glabrous throughout. Prophylls to 10 mm long, base truncate, apex narrowly acute, with very sparse glandular hairs. Leaves with petiole 1–10 mm long, slender, with sparse glandular hairs at least when young; blade lanceolate-ovate to oblong-ovate to ovate-elliptic, 6.5–15 $\times$ 2.2–5.5 cm, acute to more commonly rounded (rarely shallowly cordate), slightly unequal and occasionally minutely auriculate at base, gradually acuminate to very long-acuminate, occasionally cuspidate at apex, 5- to 7-nerved (3 most central protracted to apex), membranous, drying thin and generally rugulose (rarely bullate), appearing glabrous but with glandular hairs when young. Inflorescences 2–5.5(–6.3) cm long, white at maturity, fragrant; peduncle slender, rachis appearing glabrous but with glandular hairs; bracts broadly spatulate-cupulate to strongly cupulate (occasionally appearing



MAP 5. Distribution of *Piper yucatanense*; inset of Central America shows isolated collecting localities in Nicaragua and Panama.

petiolate), 0.25–1.5(–2) mm long, nearly glabrous. Flowers with pedicels divaricate, 1–4 mm long, very sparsely puberulent with glandular hairs; stamens 4 to 8, hypogynous, the filaments less than 0.25 mm long, the anthers subglobose, dehiscing laterally; ovary obloid to ovoid-ellipsoid, puberulent with glandular hairs, the style from $\frac{1}{3}$ to nearly equaling length of ovary, becoming largely obliterated in fruit, the stigma lobes (2 or) 3 or 4 (or 5), persistent in fruit. Fruits ovoid to ovoid-ellipsoid, to 3×2 mm at maturity, with numerous glandular hairs.

DISTRIBUTION. Most prevalent in Yucatán Peninsula, where sympatric with *Piper neesianum*; ranging naturally into western Honduras. One collection known from Nicaragua, one from Panama (see MAP 5).

HABITAT. Originally most often in “ramonales”; currently in second-growth forests with *Piper neesianum*. From near sea level to 1000 m alt.

PHENOLOGY. Flowering February to late June or early July, most commonly late April to early June. Mature fruits from August until early in next flowering period.

REPRESENTATIVE SPECIMENS. Mexico. CHIAPAS: Yaxchilán, *Breedlove* 42858 (MEXU, MO). TABASCO: 2 km [?] de Teapa, *Cowan* 3161 (ENCB, MEXU); San Isidro near Balancán, *Matuda* 3382 (F, GH, MEXU, MICH, NA, NY). CAMPECHE: 3.5 km S of Xpujil, *Bornstein & Chase* 68 (MICH); ruinas de Chicana, Hopelchén, *Chan & Ucán* 994 (MEXU); 2 km S of Xpujil, *Shepherd* 25 (F). YUCATÁN: Xcan, *Miranda* 8248 (MEXU, US). QUINTANA ROO: 1.6 km S of Santa Cruz Chico along Hwy. 307, *Bornstein & Rutledge* 23 (MICH); 0.3 km SE of km 20 marker along Hwy. 196, *Bornstein & Rutledge* 34 (MICH); along Hwy. 186 toward

Chetumal, 1 km E of intersection with Hwy. 307, *Bornstein & Rutledge 37* (MICH); 1.9 km S of Bacalar–Cenote Azul turnoff along Hwy. 307, *Bornstein & Chase 71* (MICH); 8 km S of Xactun, Felipe Carillo Puerto, *Pérez 418* (MICH); 25 km N of Cobá, *Téllez & Cabrera 2534* (MEXU). **Belize.** ORANGE WALK: Honey Camp, *Lundell 312* (F, GH, ILL, MO, NY). BELIZE: mi 24–25 on Northern Hwy., *Dwyer & Liesner 12037* (GH, MO); Maskall, *Gentle 1246* (GH, ILL, MICH, NY). CAYO: 9.5 mi S of Georgeville on road to Augustine, *Croat 23337* (F, MO); vic. of Cuevas, S of Millionario, *Croat 23629* (MO); 4 mi S of Grano de Oro on road to La Flor, *Dwyer 10906A* (F, MO, NY); Cuevas, *Dwyer 11572* (MEXU, MO); Vaca, *Gentle 2511* (GH, MICH, TEX); 6 mi S of Grano de Oro, La Flor camp, *Lundell 6289* (F, GH, MEXU (3 sheets), MICH, NY, TEX, US); Cohune Ridge, *Lundell 6499* (GH, MEXU, MICH, NY, TEX); Chiquibal Forest Reserve, *Proctor 30064* (TEX). STANN CREEK: Silk Grass Creek Reserve, *Gentle 3102* (MICH); between Silk Grass and Railway, *Sampson 12* (K (2 sheets)). TOLEDO: Columbia Forest Reserve (1–2 mi N of entrance), *Croat 24174* (MO); Punta Gorda–Seven Hills road, *Gentle 5040* (F, TEX); near San Antonio, *Gentle 7530* (GH, TEX); between Orange Point and Moho R., *Gentle 7679* (F, G, TEX, UC, US); trail from Columbia Forest Station to Esperanza, *Gentry 8171* (F, MO); Forest Home, *Schipp 506* (F). DISTRICT UNKNOWN: Prospecto–Maskall road, *Gentle 895* (GH, ILL, MICH, MO, NY). **Guatemala.** PETÉN: La Libertad, *Aguilar 251* (ILL, MICH, MO, NY); Dolores, *Contreras 2557* (NY, TEX); Lacandón, *Contreras 3412* (TEX); 1 km S of Lacandón, *Contreras 3519* (TEX); 6 km SSW of Lacandón, *Contreras 3538* (F, G (2 sheets), MICH, TEX); Macanche, *Contreras 5807* (GH, TEX); Tikal Natl. Park, *Gentry 8327* (F, GH, MO); El Paso, *Lundell 1487* (F, GH, MICH, MO, NY, US); Santa Elena, at km 38 near road to Remate, *Ortiz 2048* (F, MO, NY, US). ALTA VERAPAZ: finca Argentina above Papalja, 15 mi W of Telemán on road from Tucuru to El Estor, *Croat 41539* (MO); Cacao, Trece Aguas, *Lewton 333* (F). IZABAL: 6 km from La Ruidoza, *Contreras 10796* (MEXU, MO, TEX); Cienaga, on Petén–Guatemala road, *Contreras 10853* (MEXU, MO, TEX); ENE of finca El Zapotillo, E of El Estor, Lake Izabal, *G. C. Jones & Facey 3434* (F, MEXU, MICH, NY, TEX, US); vic. of Quiriguá, *Standley 23952* (GH, ILL, MO, NY). **Honduras.** COPÁN: between Santa Rita and Copán ruins, *Molina 30605* (F (2 sheets), MO). SANTA BARBARA: W side of Lake Yojoa, *Williams & Molina 11423* (F, GH, MO, US); near village of Las Vegas, *Yong et al. 85* (MO). CORTÉS: valley W of San Pedro Sula, *Bangham 345* (F, GH); canyon of Río Piedras, 3 km from San Pedro Sula, *Molina 3432* (F, US). COMAYAGUA: near La Libertad, *Molina 7009* (F (2 sheets), TEX); valley of Jamalteca, *Molina 7185* (F (2 sheets), TEX); Jardines, *Barkley & Hernández 40847* (GH). **Nicaragua.** ZELAYA: mountains and rain forests between Toro Bayo and Esquipulas, *Shank & Molina 4637* (F).

Piper yucatanense is, at first glance, vegetatively similar to *P. muelleri*, but it is easily distinguished by its glabrous appearance. However, several collections (*Burch 6094*, *Contreras 10796*, *Gentry 7830*, *Molina 30605*, *Standley 24675*, *Williams & Molina 11423*, and *Yong et al. 85*), primarily from the Guatemala–Honduras border, do have considerable pubescence on the prophylls, petioles, leaf blades, rachises, and bracts, reminiscent of *P. muelleri*. Fortunately, these two species can be distinguished on the basis of filament length and fruit shape, and they are geographically separated as well.

Piper yucatanense has also often been confused with its sympatric neighbor *P. neesianum*. It is distinguished from that species by its smaller, less dense habit, its membranous, rugulose (vs. coriaceous, nonrugulose) leaves, and its longer, broadly spatulate bracts. In addition, it occurs in more open areas of the forest and is not a dominant member of the understory.

Yuncker (1950), when making the new combination *Ottonia thiemeana* (Trel.) Yuncker, cited *Pittier 3458* as the type collection. This is clearly incorrect because the type must be that of the basionym, *Piper thiemeanum* (*Thieme 5455*).

ACKNOWLEDGMENTS

I am most grateful to W. R. Anderson, who unwittingly first introduced me to the family Piperaceae, for his guidance during the course of this study, for his valuable editorial assistance, merciless and otherwise, and for correcting the Latin descriptions. To W. H. Wagner, Jr., I offer special thanks for his assistance on numerous technical matters and his constant encouragement. Helpful criticism of the manuscript was provided by W. C. Burger, C. J. Humphries, and M. Tebbs.

I am particularly indebted to L. M. Villarreal de Puga, and her staff and students at the Herbario, Instituto de Botánica, Universidad de Guadalajara, for their gracious hospitality and assistance during my field studies. Thanks are also due to N. Hensold, M. Chase, and especially S. DeVivo, who accompanied me on several field excursions.

I thank the curators of A, BR, C, ENCB, F, G, GH, H, ILL, K, LE, MEXU, MICH, MO, NY, PR, TEX, UC, and US for the loan of herbarium specimens used in this study.

For their artistic skill in rendering excellent illustrations from material admittedly less than ideal, J. Charles, A. Eisenberg, and especially P. Kernan are to be commended. I also gratefully acknowledge the expert editorial assistance of E. B. Schmidt in the preparation of this manuscript.

This paper represents a portion of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree (Botany) at the University of Michigan. Financial support for this project was provided, in large part, by grant DEB-8116762 from the National Science Foundation to the University of Michigan. I also received support in the form of grants and fellowships from the Department of Botany, the Division of Biological Sciences, and the Horace H. Rackham School of Graduate Studies (all at the University of Michigan), as well as from the Michigan Chapter of Sigma Xi. Their help is much appreciated.

Last, I want to thank my wife, Nancy, for her continuous support and patience during this study.

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APPENDIX. Index to collectors.*

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*The designations in parentheses refer to the corresponding taxa in the text.

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